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Patterns of Ecological Performance and Aquatic Insect Diversity in High Quality Protected Area Networks

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To the Graduate Council:

I am submitting herewith a dissertation written by Jason Lesley Robinson entitled "Patterns of Ecological Performance and Aquatic Insect Diversity in High Quality Protected Area Networks." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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Patterns of Ecological Performance and Aquatic Insect Diversity in High Quality Protected Area Networks

A Dissertation Presented for

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ABSTRACT

Protected areas are at the heart of plans for biodiversity conservation. Networks of protected areas may provide opportunities to protect conservation targets or objectives not attainable for single parcels of land. The landscape of potential decisions available to conservation planners is constrained by uncertainty about the form of future climate states. New methods are available that can provide objective assessments of the direction and magnitude of shifts in climate regimes that are not first filtered through theoretical responses of biodiversity. Successful predictions of where, in protected area networks, climates are most likely to change, or most likely to remain *in situ,* would be valuable information for planners and conservationists. As climate change influences the potential distribution of plants and animals on the landscape, the realized effects of these changes will be determined in part by the capacity for dispersal among habitats, including protected areas. Understanding the processes that generate species diversity first requires describing the patterns; for aquatic insect species in the southeastern United States these patterns are not fully known. I describe the composition of aquatic insect assemblages in national parks as a function of the size and distance between parks, composition of regional source pools, position along environmental gradients and assessments of the perceived imperilment of individual aquatic insect species. I compare turnover among habitats and parks to test hypotheses about the partitioning of species diversity among sites, including general comparisons of headwater and mid-order streams and more explicit hypotheses on the structure of turnover along spatial and environmental gradients. Benthic data on family or genera level identifications cannot adequately test these hypotheses because the lack of taxonomic resolution obscures the sources of compositional dissimilarity between sites.

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CHAPTER I. GENERAL INTRODUCTION

The following chapter is a slightly modified version of a paper to be submitted for publication:

Robinson, J.L. and C.R. Parker. Problems and techniques for conservation of aquatic insect species, using protected area networks and macroecological methods.

Abstract

Advances in the availability and techniques of analysis of spatial data (and species occurrence records) offer opportunities for improving the conservation of plants and animals. In this review I discuss some of these advancements in the context of the conservation of aquatic insect species occurring in the highlands of the southeastern United States (insect orders Ephemeroptera, Plecoptera and Trichoptera, collectively "EPT"). I begin with an overview of historical and sociological motivations for designating protected areas and describe some general parameters of "performance" that have been considered by previous authors. Next, I describe new techniques that might aid managers in predicting where ecological changes might be most likely to occur, potentially influencing decisions about where to allocate resources and how to prioritize conservation targets. I then discuss factors that continue to limit the value of the most commonly collected aquatic insect occurrence and abundance data, and elaborate on how these limitations might obscure ecological patterns that are interesting not only for conservation purposes but also relate to more general questions in ecology. I then provide examples of how I have quantified these patterns in some networks of high quality protected areas in

the region, national parks in two monitoring networks, that jointly protect many unique habitats and environmental features that are far less prevalent and protected outside of lands in these networks.

Background

Recent innovations in the analysis and availability of ecological and spatial data, particularly the increasing availability of digitized museum records, have opened new frontiers in biodiversity assessment and conservation planning. Immediate expert application of these methods is needed to mitigate problems stemming from shifts in spatial patterns of the growth of human populations, changes in climate patterns and increases in land uses linked to the degradation of ecological systems. The enormity of the conservation challenges posed by changing climates and landscapes should prompt inquiry on the adequacy of current conservation plans to protect ecological targets, particularly those linked to the delivery of ecological goods and services to human populations.

In the United States, land acquisition has been a successful baseline strategy for resource conservation (Groves 2000). Networks of conservation lands play a necessary role in protecting ecological targets or objectives under climate change (Rodriques 2004, Gaston 2008), but simple land possession alone will not be sufficient for protecting biodiversity under changing climatic conditions (Kostyack et al. 2011). For conservation practitioners, implementing forecasts of future climatic or ecological conditions into management proscriptions is limited by several factors, including uncertainty regarding current system states or trajectories (Beaumont 2008, Felton 2009, Real et al. 2010),

epistemic limitations of analytical and predictive tools (Araujo et al. 2004, Nenzen and Araujo 2011, Ellis 2011) and bureaucratic or institutional inertia (Jantarasami et al. 2010).

Adaptive management strategies for plants and animal conservation draw upon a wide spectrum of ecological theory: the demographics of dispersal, landscape measures of spatial connectivity, community assembly theory, niche modeling and keystone ecological interactions. This dissertation is an effort to describe and develop a new approach for predicting where and how climate change might affect protected areas, and to provide a macroecological perspective to freshwater aquatic insect conservation that builds on the results of a biodiversity inventory of seventeen key protected areas in a region of exceptional taxonomic and phylogenetic diversity of aquatic insects.

Motivation for protected area conservation

"Protected areas" can be protected in many ways and for many reasons. Throughout human history, the oldest "protected areas" are probably areas that were held in commons by nomadic or agriculturalist societies, such as hunting or fishing grounds. Other types of protected areas may have been held as taboo, where entry was regulated for mystical or religious purposes. In recent history, places have come to be protected under common laws and mutual consent between governing bodies. Lands held in common have largely disappeared from the western world, replaced by private property and lands held in trust by government bodies. Changes in stewardship and use patterns are necessarily accompanied by changes in ecological patterns of plants, animals and human uses of these

lands. Perhaps less often do biologists or resource managers consider that changes in stewardship are frequently associated with shifts in human social structures or relations in populations living in (or displaced from) protected areas (e.g., Hughes 2005, West et al. 2006). Recognizing that ecosystem responses to perturbations are inextricably bound up with past and present human influences on these ecosystems is a critical dimension of anthropological studies, but ignored by protected area designations that perpetuate mythical narratives of untrammeled wilderness and uninhabited nature (Cronon 1995).

The 20th century has seen the proliferation of many different categories of protected areas in the US, administered under the authority of local, state and federal government agencies as well as non-governmental organizations (NGOs) and private landowners. Growing public recognition of the value of lands set aside (including the emergence of a distinctly American "land ethic" (Leopold 1956)) has been a driving force in the creation of protected area networks, such as the National Park Service, beginning with the official designation of Yellowstone National Park in 1872. Yet much of this planning and acquisition has been perpetuated without considering the long-term ecological benefits of land preservation (Scott et al. 2001). Although it is not always obvious to visitors and users today, much of the vast tracts of land protected by the US Forest Service in the eastern US were degraded "lands nobody wanted" (Shands 1992). Since quantitative attempts to objectively evaluate reserve design, or analyze trajectories of climate or land use change, are relatively recent developments hastened by the advent of computerized scientific investigation, these disciplines could not have greatly influenced the designation or management of the bulk of pre-existing protected areas.

In order to predict whether protected areas can maintain current functions (e,g,, provide ecosystem services or create habitat for rare species) it will be necessary to model the performance of these areas in possible future climatic and ecological configurations. "Performance" is a necessarily subjective analysis, since it assumes the existence of some criteria, system or phenomenon (Gaston et al. 2008). In this dissertation, I offer a new criterion for measuring the performance of protected areas, specifically the context of landscape similarity of protected area climates, a measure I call the "climate footprint" of a protected area.

Chapter II

Tailoring species-specific ecological analyses to any particular biogeographic setting is an exercise in contingencies. Even if ecological niche models, for example, accurately describe a correlative relationship between the distributions of some species to some set of environmental features, these features may not predict local abundance, total population size, dispersal capacity or the outcome of ecological interactions (Lawler et al. 2011). Processes governing the formation of ecological communities in future climates are likely to be more complex than the simple sum of individual climatic responses of individual species (Keith et al. 2009). Extrapolating predictions of "presence" into species-interactions in communities with no contemporary analogs adds additional uncertainty into these analyses (Urban et al. 2012). Estimates of the niche occupied by species are constrained by the data used to estimate the niche, and thus likely to always be biased by factors beyond the consideration or data availability of scientists seeking to answer these questions (Godsoe 2009). It seems that planning solutions provided by reductionist, single

species approaches under current conditions might have limited applicability to future ecological problems in future conditions. On the other hand, what other options are available?

In this dissertation I suggest that models developed to describe species distributions and project environmental relationships onto future conditions may be useful in ways that have not yet been explored in the ecological literature. It is true that the boundaries of species distributions do not necessarily respect political or administrative boundaries, with the consequence that the realized level of conservation protection for some species may change as actual distributions change under climate change or as a result of major land use changes. With the exception of lands near shifting coastlines, protected area boundaries will not change with climate or land cover conditions. So, the "real estate" occupied by protected areas is a stable anchor point for analyzing ecological change: protected areas have direct relationships to climate features that are determined solely by geographical position and not by biological processes. These relationships in turn provide the template to biological processes that bound the possible responses of any species to changes in environment. I show that when used in this manner, these models deliver generalizations about the landscape context in which protected areas are embedded that may be relevant to species, community and ecosystem planning.

The climate footprint of a protected area is estimated from predictions from ecological niche models, using gridded environmental data, or from spatial statistic measures of similarity (Fig. 1). If predictive models (e.g. MaxEnt, Phillips et al. 1996, Phillips and Dudik 2008) are used to estimate the distribution of the climate footprint, then

transferring those predictions to some set of future climate conditions is a straightforward application in MaxEnt. Interpreting predictions of future climate suitability for species distributions requires biological assumptions about the ecology of species (i.e. dispersal to suitable areas is possible, or that climate features are strong determinants of distribution and not intraspecific interactions) that are not required for models of the climate footprint of a protected area. In either application, MaxEnt users may tune models to make binary predictions based on probability thresholds that are either user-defined or derived from information theory.

One such threshold is designed to minimize the rate of false negatives (predictions into regions that are actually unsuitable for a species), which requires knowledge of "absence" or firm confidence in the estimation of the niche breadth, conditions unlikely to be met for species distribution modeling. These assumptions are not required to model the climate footprint of a protected area; since the boundary of the protected area is known with absolute confidence then this offers a solid empirical justification for theoretical thresholds that is not available within species distribution modeling, where distributions are much less certain.

A useful feature of this technique is that it provides a potential metric for assessing the connectivity between protected areas. Whether protected areas are likely to function as *in situ* refugia, or whether corridors of similar climates will exist between protected areas based on the climatic features, may be answered on the basis of the landscape context of the protected area alone without the uncertainty introduced by projecting species niche models into future conditions. These are novel tools for evaluating the

performance of protected areas as *in situ* refugia or corridors connecting regions of similar climates, a critical (and often overlooked) component of conservation plans under climate change (Hodgson et al. 2009, Krosby et al. 2010). Within a network, efforts to enhance the connectivity of protected areas can use these methods to prioritize the allocation of conservation dollars towards connecting particular protected areas predicted to lose climate footprint connectivity or with little *in situ* refugia.

Chapter III

Another major development in this work is the application of ecological theory and analysis to ask if protected area networks function as reserves for imperiled aquatic insect species in a region noted for exceptional patterns of phylogenetic and taxonomic diversity. Aquatic macroinvertebrates are the direct target of an enormous amount of field and laboratory research, implemented through biological monitoring programs directed by many levels of government, non-governmental agencies, academic research and even community organizations (Kenney et al. 2009). Monitoring programs use these data to assess water quality, by relating observed patterns of macroinvertebrate taxa to patterns expected from empirical and theoretical predictions. The success of these programs is astounding considering that advances in this field have been made on the basis of ignoring the identity of the species that are collected. Immature life history stages of freshwater aquatic insects are often not identifiable below family or genus levels of taxonomy (Lenat and Resh 2001, Merritt et al. 2008). The science of benthic macroinvertebrate monitoring is an exercise in "species-free" biological theory.

Yet, it works! The morphological and ecological conservatism among higher clades EPT taxa is a remarkable feature of the biology of aquatic insects (Poff et al. 2006). Although there are many exceptions to broad genus or family level generalizations (Cummins 1973), organizing benthic assemblages into this pseudotaxonomy yields robust predictive relationships about ecological function or pollution tolerance (Cummins and Klug 1979, Menezes et al. 2010). There may be no other extant group of macroscopic plants or animals with such a discrepancy between the (small) amount of knowledge regarding the biology of species and the immense body of knowledge on the responses to ecological factors occurring among higher taxa. However, among these trophic or functional feeding groups, only *species* are united by a common phyletic history, demography, reproduction and a unique taxonomic referent. Integrating these disciplines has the potential to inform many debates across ecology and evolutionary biology that are currently outside of the grasp of benthic science.

To that end, I have applied ecological analyses to aquatic insect community data that are not broadly used among benthologists. Since the focus of my research has been to establish patterns of abundance among *species*, I have necessarily employed methods not typically used to characterize benthic community composition. As a consequence, these results are not immediately transferable to measures of biological integrity or community composition that rely on benthic collections, although some exploratory work in this direction suggests that adult insects might be useful for biomonitoring purposes (Houghton 2006, Houghton et al. 2011). The questions I address in these chapters require the estimation of regional pools of species that might occur within the parks in our study area,

but such data (species-level occurrences of aquatic insects) are only available from museum records or systematic specialists or the scientific literature generated from these sources. It remains an issue that we have no finer resolution on the distribution of EPT species than state lists compiled from the work of many disparate researchers and methods. Estimates of the degree of imperilment or threats to the viability of populations of rare species are based on similarly sparse data. Formulating more robust criteria for evaluating the rarity of aquatic insect species has been one motivator of this dissertation research.

In general, a lack of comprehensive assessments of the status or viability of populations or species constrains the efficacy of conservation efforts for many taxonomic groups of plants and animals (e.g. Vieites et al. 2009). For insect species (or arthropods in general) this knowledge gap can be immense (Cardoso et al. 2011). New species of caddisflies, mayflies and stoneflies continue to be discovered or described from the eastern United States every year, including as a product of the research I report in this dissertation. In addition to discoveries of unknown species, recently published species lists for southeastern states list many new records and known range extensions of species into areas where they were previously uncollected (Lenat et al. 2010, MacCafferty et al. 2010, Floyd et al. 2012). This uncertainty in how many species are present across large areas or regions poses a serious obstacle to efficient and effective regional conservation accounting, particularly since levels of protection afforded to plants and animals are not consistent across the full geographic range of species with ranges that cross political boundaries (Rodrigues et al. 2004). This dissertation research was motivated, in part, as a biodiversity

inventory of aquatic insects in 16 national parks across the Southern Appalachian highlands and outlying areas. These parks are organized into 2 different networks, based on geography and biological characteristics and administrative fiat.

US National park lands are typically managed for restricted public uses and a high level of protection for natural and cultural resources within their boundaries. This level of restriction on activity is typically assumed to transfer directly to increased protection of individuals, populations and communities of species occurring on these lands (Gaston et al. 2009), which might be expected to result in higher species richness or prevalence of rare or sensitive taxa. Indeed, some species of EPTs are known only from national parks and might in fact be endemic to these parks. However, I present evidence in this dissertation that these instances are not typical for national parks in these protected area networks. To our knowledge, our collection efforts may be the first collection efforts in some of these parks, thus we have no information about long term trajectories of community patterns or any independent estimates of species richness or community composition in these parks by which to scale our own assessments. The information base on occurrences of species in national parks might well be larger than for other federal land holdings (Stein and Davis 2000), a sobering thought when one considers the vast tracts of land possessed by Department of Defense, Bureau of Land Management and US Forest Service agencies alone (Groves et al. 2000, Stein and Davis 2000).

Even when data on aquatic insect communities do exist, within these networks of national parks, often quality of this information is such that it cannot be used to assess conservation objectives. Routine benthic monitoring programs do exist in several of these

parks, particularly larger parks like Great Smoky Mountains National Park, the Blue Ridge Parkway and Big South Fork National River and Recreation Area. But these efforts, generally, do not provide information on *taxonomic species*, the unit of conservation used by legislation like the Endangered Species Act, state Natural Heritage Programs or global efforts like NatureServe. Biological monitoring data from streams and rivers utilizes immature forms of aquatic insects, wholly (or nearly so) aquatic life history stages, which are usually only diagnosable to genus (sometimes family), even by taxonomic experts. The result of this disconnect is that the vast body of knowledge on the ecology of aquatic insects, in immature life history stages, is not directly applicable to delineating conservation objectives for aquatic insect species.

Chapter IV

Aside from assessing the conservation value of EPT assemblages, data on taxonomic species allow direct measurement of the similarity of assemblages or communities across different habitat types and across regions. By utilizing genus and family level taxonomic data, estimates of taxa richness or turnover among samples or regions have been biased, to an unknown degree (e.g., Clarke et al. 2010, Sokol et al. 2011, Finn and Poff 2011, Finn et al. 2011, Maloney and Munguia 2011). The decay of similarity of communities or assemblages (i.e., samples) along prescribed geographic or environmental gradients is a fundamental measure in ecology (Nekola and White 1999, Legendre et al. 2005, Soininen et al. 2007). These measures may reflect the operation of metacommunity processes like dispersal limitation, species sorting along environmental gradients or habitat filters, or be a function of sites situated along varying geographic range sizes of target taxa (Harrison and Cornell

1993). A full account of winged and immature dispersal of aquatic insects is a critical (and conspicuously absent) component of understanding the assembly of aquatic insect communities, a topic critical to biological monitoring applications that summarize the responses of multiple species to stressors or gradients. Stream monitoring and restoration practices have been criticized as a "field of dreams", where dispersal into restored habitats is assumed to be inevitable (e.g.,"if you build it, they will come" (Palmer et al. 1997)). Extending this analogy, a major problem is that benthic surveys are never enough to tell you who "they" are, and our understanding of what drives successful dispersal and recruitment (what "it" is) is woefully inadequate.

Filling in these gaps will require coordinated sampling of aerial and immature life history stages of aquatic insects. Sampling aquatic stages remains critical because most of the ecological functions are carried out by aquatic insects during these stages of development (e.g., organic matter processing, transferring biomass to higher trophic levels); adult winged stages of many species in several orders are short in duration and adults may not even feed (Merritt et al. 2008) . Thus it seems intuitive that the bulk of any species sorting or habitat filtering effects must then take place in the interval between successful ovipositing of eggs, and recruitment to winged reproductive stage. If recruitment failure is correlated with environmental features (i.e. more prevalent among some habitats) then these habitats could be demographic sinks. In such a case, benthic surveys might regularly collect immatures of these species in these [sink] habitats, where interspecific ecological interactions promulgated by sink species might influence the recruitment success of other species, yet these populations contribute little or nothing to

the maintenance of breeding populations in other habitats. Similarly, if adults are collected in habitats where immatures are never found, then we might infer that rates of propagule delivery (i.e. active winged dispersal from other habitats) are inconsistent with immature abundance, as predicted by mass or rescue effects. Most importantly, as molecular genetics continue to develop more powerful tools for examining intraspecific or population level variation, quantifying effective rates of gene flow can provide the last missing piece of this puzzle: how these processes bear on the genetic composition of future populations. The complexity of life history strategies of aquatic insects, coupled with the large variation in individual reproductive success and observed intraspecific levels of divergence in mitochondrial genomes within many species (Zhou et al. 2011), are patterns that demand explanation using the full arsenal of tools supplied by ecology, evolutionary biology and spatial analysis.. This dissertation is an effort to begin that task.

Future directions

I am continuing my efforts to compile records of species occurrences from collection and museum holdings throughout the United States, and aquatic insect distributions in relation to losses from land use and projected shifts in habitat suitability associated with temperature and precipitation changes due to climate change. This applied research will expedite the process of generalizing the geographic range of EPT species with GIS and distribution models. The "range" of species has been termed the "basic unit of macroecology" (Brown 1995) and represents the cumulative sum (or running total) of all

ecological and evolutionary processes acting on the member individuals of a species. At the appropriate spatial scales, predicted geographic ranges may be compared to observed distributions of species to infer patterns of range loss coincident with correlates of environmental or ecological change, to identify dispersal barriers, and when used with phylogenetic or morphometric data may be used to test hypotheses on trends in niche evolution, trophic function and species diversification along spatial or environmental gradients.

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APPENDIX I. Figure

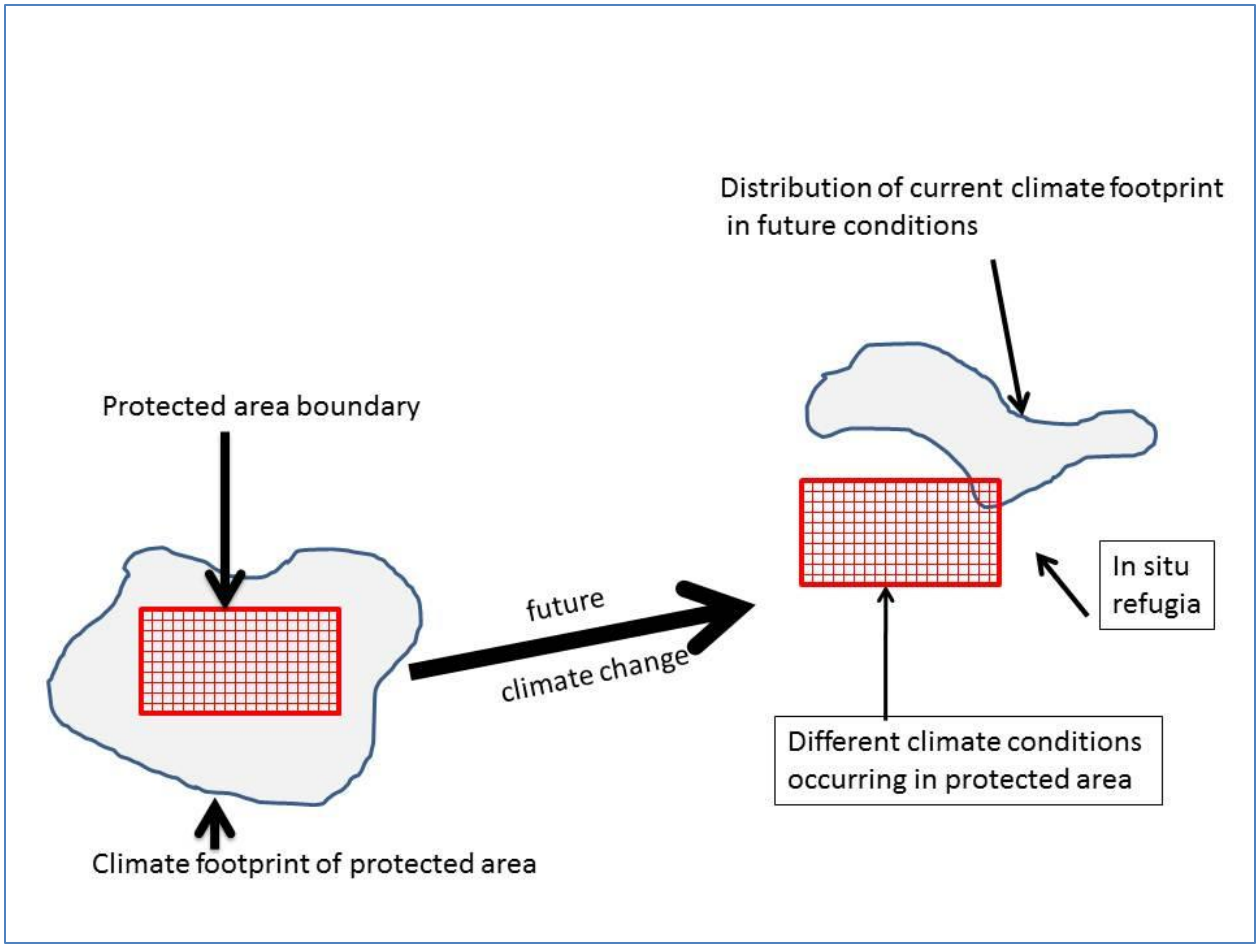

Figure I-1. Illustration of the climate footprint of a protected area. The climate footprint is the geographic extent of climates similar to those occurring in a protected area. Climate similarity may be derived from distribution model predictions or from other spatial statistics. The climate footprint of a protected area may be very large (if the protected area occurs in a homogenous region) or very small (protected area is an island of unique climate features surrounded by climate heterogeneity). *In situ* climate refugia occur where current climates persist in the protected area into future conditions.

CHAPTER II. A METHOD FOR PREDICTING *IN SITU* CLIMATE REFUGIA AND FUTURE CONNECTIVITY IN PROTECTED AREA NETWORKS

This chapter is a slightly modified version of a paper to be submitted for publication.

Robinson, J.L., A. Bartley and J.A. Fordyce. A method for predicting *in situ* climate refugia and future connectivity in protected area networks.

Abstract

Planning for climate change effects to the distribution of plants and animals in protected area networks will require strategies that maximize the connectivity among units and minimize uncertainty around whether units can provide sufficient quality habitat to maintain viable populations of target species. Previous attempts to evaluate protected areas on the basis of future habitat characteristics have relied on species distribution models that relate species occurrences to temperature and precipitation patterns, then project the relationships among these variables into future climate conditions. Such analyses have found that many species distributions may change to the degree that they will no longer have suitable habitat within protected area boundaries. I offer here methods that directly estimate the geographic distribution of climate states occurring within protected areas (i.e., the "climate footprint of a protected area") without the potentially confounding filter of the distribution of species ranges that may not be completely determined by temperature and precipitation patterns. I use these methods to evaluate the predicted dynamics of climate footprints in future scenarios, specifically: expansion, contraction or extinction of climate footprints of protected areas, capture of climate

footprint by boundary of other protected areas in network, and the prevalence of *in situ* climate refugia where climate footprints persist into future conditions.

Introduction

Unquestionably, the anticipation of ecological impacts as a result of climate change has hastened a new era of conservation planning. The inherent spatial complexity of ecological systems is a challenge to systematize planning to protect biodiversity even under the assumption of equilibrium, but the uncertainty around the state of future climate patterns compounds these challenges. Statist command and control bureaucratic structures, with limited flexibility for adapting plans once in motion, may produce a lack of clear management directives for planners and managers (Lawler 2009). Planners may lack confidence in pursuing aggressive or risky strategies to protect ecological resources from climate change, inhibited by a lack of information about the local or regional outcomes of climate change that would help to distinguish between resource management options. Alternatively, institutions may have organizational inertia due to internal policies or external regulatory environments (Jantarasami et al. 2010).

Parsing scientific uncertainty from political expediency or institutional uncertainty is probably a role best played by sociologists or public relation strategists, but creating tools to quantify the domain of that scientific uncertainty is a legitimate role for ecologists. Many effects *could* result from changes in spatial and temporal patterns of temperature and precipitation: repositioning of the geographic distribution of suitable habitats, shifts in the

realized outcomes of ecological interactions among and between individuals or species, or changes in the phenology or behavioral traits of breeding populations of organisms. However, the primary tool for predicting the effects of climate change on the distribution of species remains limited by confidence around predictions of which of these effects are most probable (Real et al. 2010). Projections of the dynamics of species' geographical ranges (expansion, contraction or extinctions) may vary with climate scenarios (Beaumont et al. 2008) modeling methods (Lawler et al. 2006, Henzen and Araujo 2011), or across networks of protected areas or land holdings encompassing biogeographic transition zones (Griffith et al.2009).

This uncertainty around ecological responses to climate change is a function of both "known and unknown unknowns". The domain of current climate states limit the range of observations of the behavior of species, communities or ecosystem; extrapolations away from these conditions require assumptions that may have varying evidential support. When possible, extrapolations may be made on the basis of experimental results. For example, the physiological tolerances of a species may be tested in laboratory or mesocosm experiments, providing an empirical basis for predictions on the response to climate change (e.g., Dole et al. 2003). Alternatively, the assembly of ecological communities in future conditions may be shaped by differential dispersal pathways or interspecific interactions (Gilman et al. 2010, Keith et al. 2008, 2011, Urban et al. 2012) and thus less influenced by temperature and precipitation patterns than

single species distribution models predict (even when these predictions are consilient among modeling methods (Real et al. 2010)). The lack of analogous communities, in current climate or landscape configurations, will limit the effectiveness of climate change conservation plans made on the basis of current species distributions alone (Strange et al. 2011).

Many investigators have emphasized the importance of connectivity among protected area networks to sound conservation planning (Rodrigues et al. 2004, Gaston et al. 2008, Griffith et al. 2009, Heller and Zavaleta 2009, Lawler 2009, Krosby et al. 2010), but these analyses remain focused on the response of *species* and thus tailor recommendations to managers of protected areas on the basis of protecting communities or populations designated as conservation targets *a priori*. Yet, the realized geographic distributions of climates in future conditions may result in the loss of suitable habitats from protected area networks, if regional climates are replaced by non-analog conditions or if current protected area climate conditions migrate out of the boundaries of protected areas into regions with no protected areas. In these instances, species distribution models may fail to accurately assess the suitability of future conditions across all protected areas, or may yield inconsistent predictions (Real et al. 2010).

As climates shift away from current conditions, the distributions of many species are certain to change or are already changing in response (Walthe *et al.* 2002; Parmesan and Yohe 2003; Parmesan 2006). The geographic boundaries of

protected areas and reserves remain fixed, posing a fundamental question to any conservation plan: is it preferable to manage for current ecosystem configurations, or to plan for future conditions? Management proposals designed to conserve particular populations or communities might be compromised if the actualized effects of climate change shift environmental conditions far outside of the abiotic requirements for individual organisms. Increasing the connectivity between reserves or protected areas might protect populations of target species (Heller and Zavaleta 2009; Krosby et. *al* 2011), but may not provide as many desired benefits as increasing the size or quality of existing reserves (Hodgson et. *al* 2009). Even in instances where increasing connectivity is a preferred option, it would be useful to know (under a climate change scenario) which reserves, corridors or geographic areas are likely to occupy climatic conditions conducive for dispersal or occupancy.

Here I use MaxEnt, a maximum entropy modeling technique, in a novel application for predicting the dynamics of the climates occurring in protected areas under climate change. The degrees of connectivity between protected areas, or whether protected areas might retain current climate conditions in situ, are determined in part by the spatial context in which protected areas occur. A protected area with climate features unique to the protected area (e.g. captures a mountain range or other topographic features) might be of greater conservation significance than a protected area that is broadly similar to a large region of similar climate. This spatial context I have termed the "climate footprint" of a

protected area, specifically the geographic extent of the suite of values of climate variables that specify a particular geographic area in a predictive model. The domain of these values is the "climate space" occupied by a protected area. The overlap between the climate footprint of a protected area in current and future conditions is a measure of the area with similar climates that might be expected to persist *in situ* under climate change (Fig. 1).

As a species distribution model, MaxEnt uses spatial coordinates of species occurrences and environmental covariates to predict the distribution of a species across a larger area or set of environmental features (Elith et al. 2011). There is nothing inherent in this approach that limits this modeling technique to the occurrence of plants and animals, and in fact several assumptions required by this method (as a species distribution model) are not necessary when this method is used to model the climate footprint of predicted areas. For example, MaxEnt tunes model parameters against "pseudoabsences" randomly drawn from the background of environmental data, where the species is assumed to be absent (Phillips et al. 2006). Depending on the quality of the occurrence data, this assumption may or may not be met (i.e. undetected presences may be sampled as pseudo-absences, which will certainly reduce the environment-presence relationship in the model), but modeling the climate footprint of a protected area eliminates this uncertainty, since the boundaries of parks can be known with absolute confidence.

To illustrate this method, I used MaxEnt (3.3k, Phillips et al. 2006) to analyze the climate footprints of 163 national parks in the conterminous United States, under current conditions and in two future (2050) climate projections (emissions scenarios a2a, b2a; Hijmans 2005, Ramirez and Jarvis 2008). I test hypotheses on the relationships between park area, the number of ecoregions occupied by parks, the area of the current climate footprint, the area of the future climate footprints, probability of extinction of the climate footprint of each park and the area of *in situ* climate refugia provided by parks.

Methods

All spatial analyses were performed in ArcGIS 10 (ESRI). Data for national park boundaries were obtained from the National Park Service Research and Innovative Technology Administration Bureau of Transportation Statistics, maintained by the Louisiana Geographic Information Center, available online at http://lagic.lsu.edu/data/losco/national_parks_boundaries_bts_2006_faq.html, accessed Jan. 4 2012). I downloaded a shapefile of Bailey's Ecoregions of the United States from the National Atlas (Bailey 1995) to summarize dynamics of prevalence, expansion, contraction and extinction of climate footprints and *in situ* climate refugia, and downloaded the 19 BIOCLIM variables, in 1 km^2 gridded environmental layers, for current climate conditions from WORLDCLIM (Hijmans 2005) and statistically downscaled future scenarios from the International Center for Tropical Agriculture (Ramirez and Jarvis 2008; climate

scenario SRES A2a and B2a, HADCM3). I clipped the environmental layers by a shapefile of the conterminous 48 states, to define the environmental background for modeling.

To obtain spatial coordinates for use in MaxEnt, I used ArcGIS to select the centroid of all raster cells a buffer distance of $\sqrt{2}/2$ kilometers from the park boundary. This ensured that I captured all raster cells with any amount of park boundary. I eliminated raster cells within 5 km of coastlines to eliminate discrepancies between models and local climates related to lake or ocean effects that may not be captured in the large-scale models. I eliminated all parks in at least 20 pixels to reduce effects of small sample sizes on model performance (Pearson et al. 2007), leaving 163 parks with area at least 20 km^2.

I used MaxEnt to build models of the climate footprints of these national parks (increasing the number of background points to 10,000 in MaxEnt options), then applied a probability threshold (maximum sensitivity + specificity) to transform the raw output into a gridded binary prediction surface. This threshold uses characteristics of the receiver-operating curve to maximize the prediction rate of true negatives and true positives to minimize commission and omission error rates (Jimenez-Valverde and Lobo 2007). Although recommended by previous studies for models where "true" absences are uncertain since species distributions are not completely known, in our approach this feature is empirically justified since the distribution of national park

boundaries are known with absolute certainty, effectively eliminating any uncertainty around the actual rate of true negatives.

Next, for each park in the network, I projected models of the current climate footprint models onto future conditions and measured the change in the size of the footprint in future conditions. I used the GIS to find the centroid of the current and future climate footprints and the R package *fields* (Furrer et al. 2011) to measure the great circle distance between the centroids current and future climate footprints. I used Geospatial Modelling Environment (Spatial Ecology 2012) to compute the number of climate footprints in each ecoregion polygon. I log transformed the square root of the area of park boundaries and climate footprints to approximate normality, then used linear and logistic regression to explore relationships among variables.

Results

Among 163 national parks, park area ranged from 20 to 20,614 km^2, with a median area of 233 km^2 (Table 1). The median climate footprint area, in current conditions, was 27.2 times larger than the associated park area (range 3- 801). The cumulative density of park climate footprints ranged from 0 to 7, with the greatest fractional area predicted in ecoregions in the western deserts, the Everglades and Appalachian ecoregions (Fig. 2).

Parks occupying multiple ecoregions had significantly larger climate footprints than parks in a single ecoregion (ANOVA, $F_{1, 159} = 20.8$, Tukey's HSD

p<0.0001), but were not less likely to go extinct in a2a (Likelihood ratio test, χ_2^2= 2.0, p= 0.36). In b2a climate footprints of parks occupying more ecoregions were more likely to go extinct than parks in a single ecoregion (Likelihood ratio test, χ_2^2= 6.1, p= 0.05). Larger parks had larger climate footprints in current conditions (log transformed square root; $F_{1, 162}$ = 350.2, p<0.0001, r^2= 0.69), but park area was not related to the future climate footprint size in either scenario a2a ($F_{1, 139}$ = 1.6, p=0.21) or b2a ($F_{1, 47}$ = 0.26, p=0.61). Larger parks had climate footprints which were less likely to go extinct in both the a2a (χ_1^2 = 4.4, p =0.04) and b2a (χ_1^2 = 4.7, p =0.03) scenarios.

Climate footprint extinctions occurred in both future scenarios but were much more prevalent in the b2a scenario (114 extinctions) than in a2a (22 extinctions). Among parks with climate footprints that did persist in future conditions, the future climate footprint tends to occupy much larger portions of the study area than under current conditions (some four or five orders of magnitude larger than the area of the park). In the a2a scenario, in 2050 park climate footprints accumulate in the greatest density in the southeastern US, although some map pixels in the southwest capture as many as 10 unique climate footprints in the same pixel. However, in this scenario many pixels are not predicted to be occupied by the climate footprint of any park (Fig. 3). The scenario b2a predicts the accumulation of more climate footprints across the study area, with the result that all portions of the study area are predicted by at least 2 and as many as 23 different park climates (Fig. 4).

In situ climate refugia were nearly seven times as prevalent, in the a2a scenario, than in b2a. Close geographical proximity increases the likelihood that climate space, species assemblages or other properties are shared among protected areas, a justification for aggregating protected areas in networks. The spatial structure of networks will influence whether climate footprint dynamics associated with changing climates will result in capture of climate footprints by protected areas within or outside of particular networks. The western United States has a number of large national parks in close proximity, spanning multiple monitoring networks. The connectivity of these regions by the Rocky Mountain massif might create conditions with conservation implications across networks (Fig. 5). The a2a scenario models predict that these parks in this region have the potential to maintain current climate configurations into 2050, and some areas in the region might in fact provide *in situ* climate refugia for more than one protected area simultaneously. These areas could be superior candidates for translocation or assisted migration of populations that are imperiled in other portions of the southwest, or might be priority targets for additional land acquisition.

At a smaller scale, and within a single network (Appalachian Highlands), climate footprint dynamics in the Southern Appalachians may yield insights to successful management strategies. Refugia identified in these models remain in network, even when they no longer occur in those parks. In particular, the climate footprint of the Blue Ridge Parkway may not only persist *in situ* but

climates from the surrounding parks in network also accumulate in that footprint (Fig 6, a-d).

Discussion

These methods may be helpful to conservation practitioners and protected area managers, if they describe the possible trajectories of ecological dynamics resulting from climate change on lands managed for conservation. The tradeoffs inherent in planning for future climate states or ecological configurations, at the expense of current configurations, require the investment of capital, labor and institutional resources with limited confidence in the benefits or returns. One way to alleviate some of this uncertainty is to provide objective assessments of the performance of protected areas. Certainly, protected areas may be valuable on the basis of multiple criteria, but habitat for species is one of the most basic services offered by any managed lands. However, management plans built around maintaining the current composition of species might compromise the prospects of protecting immigrating species (Strange et al. 2011), some of which might be desirable conservation targets in their own right. We suggest that if it is possible to quantify the *potential* for some region or area to act as habitat for some species that this information would inform strategies by ruling out unlikely scenarios or providing a calibration for comparing among competing plans.

Previous researchers have constructed accounts of the baseline abiotic conditions, in regions of interest, in order to describe the potential trajectory and magnitude of shifts in climatic conditions associated with changing temperature and precipitation regimes (e.g. Ackerly et al. 2010, Beaumont et al. 2011). The methods I describe here depart from these approaches in that they consider the landscape context of climates surrounding protected areas, to explicitly evaluate change in the spatial distribution of climates currently under protection. Tools at these scales of analysis are needed in conservation planning (Kerr et al. 2007): when applied to particular protected areas, with ancillary biological data on the distributions or ecological affinities of species, these techniques can generate testable hypotheses or suites of potential solutions to climate change challenges that are independent of controversial niche-based assumptions that drive models of the distributions of organisms.

Distribution modeling techniques can benefit conservation planning without actually modeling the distribution of species. The techniques I present here can improve the management of species that have small population sizes, geographic ranges or limited capacity for long distance dispersal by objectively characterizing the spatial extent of the landscape with climatic properties similar to protected areas and identifying potential connective corridors or regions. Authors calling for increased protected area connectivity strategies have consistently noted that such methods might benefit multiple species simultaneously (Taylor et al. 1993, Heller and Zavaleta 2009, Krosby et al. 2010). While general strategies such as "increase

connectivity among protected areas" are intuitively appealing, others have noted the increased costs associated with connectivity planning (Simberloff et al. 1992, Hodgson et al. 2009), or that uncertainty about the efficacy of increased connectivity as a mechanism for protecting populations limits the generality of proscriptive measures in general (e.g. Simberloff and Cox 1987, Araujo et al. 2004, Gaston et al. 2008, Felton et al. 2009). Identifying *in situ* refugia might reduce this uncertainty and provide empirical justification for aggressive management strategies for biodiversity targets of particular taxonomic or conservation value.

These results suggest that many national parks in the conterminous United States currently protect climate conditions that may no longer exist, within those parks, in the near future. If global change shifts the distribution of climate states currently experienced within protected areas to areas outside of protected area boundaries, the effectiveness of strategies aimed at maintaining species assemblages or ecosystem services might be limited (Krosby et al. 2010). Many national parks will likely experience climates outside of the range of current conditions or for which no analogous climate states exist within entire ecoregions. Unpredictable ecological responses to non-analog climates will challenge management for particular communities or assemblages (Fitzpatrick and Hargrove 2009), even though community assembly processes generating non-analog ecological configurations are likely to be common in geological time scales (Keith et al. 2009). In this analysis, the prevalence of park climate footprint extinction, in future scenarios, implies that these problems of non-analogous climates and species

assemblages may be inevitable in these networks. Geographic boundaries of protected areas will not shift with changing climates; these predictive techniques can be used in concert with more descriptive methods (Saxon et al. 2005, Ackerly et al. 2010) to provide a spatial context for predicted changes in temperature and precipitation regimes expected inside protected areas.

In this paper I have explicitly ignored biological interactions. Understanding how changes in abiotic conditions can and do influence the strength and magnitude of interactions between individuals, populations and species is a long-standing goal of ecology (e.g., Connell 1961, Sutherland 1974, Werner and Gilliam 1984, Dunson and Travis 1991, Wiens 2011). It's important to emphasize that understanding how abiotic regimes are likely to shift does not do much to predict how species distributions will respond, particularly since the strength and direction of interactions can change with abiotic factors in contingent ways. Yet, overlap between current and future climate states might be a useful predictor of where things are *least likely* to change, relative to other areas in a protected area. I maintain that this information might be useful in conservation contexts, even when little else is known about ecological patterns in such an area.

Current spatial configurations of protected areas and reserve networks in the United States have not been designed specifically to protect biodiversity from the effects of climate change. The large fraction of biodiversity that occurs outside of protected or managed areas will not receive additional protection from site-specific

management unless connectivity persists among reserves (Mittermeier et al. 2003, Rodrigues et al. 2004, Hannah 2008, Lawler 2009, Ashcroft 2010). In general, national parks alone might not provide *in situ* refugia for most biologically important or spatially rare climate space. Effective climate conservation strategies for mitigating biodiversity loss due to climate change will necessarily demand landscape scale planning, enhanced cooperation and dissemination of information among governmental and non-governmental agencies (Mastrandrea et al. 2010). Considering the landscape context of the climatic properties of protected areas can easily be implemented into existing management strategies for any network of protected areas or reserves and may provide new insights into strategies for protecting biodiversity in changing climates.

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APPENDIX II-A. FIGURES AND TABLES

Table II-1. Climate footprint dynamics of 163 national parks for two future climate scenarios.

Park ID	Park Area (km^2)	Ecoregions	Current Footprint Area	a2a Footprint Area	b2a Footprint Area
ACAD	106	1	988	1697	0
AGFO	47	1	970	1815	351863
ALFL	20	1	589	411216	0
ALPO	48	1	5288	94667	3447421
AMIS	690	1	6697	32	0
APCO	22	1	2724	28087	10906878
APIS	324	1	14284	0	0
ARCH	565	1	7951	15912	0
BADL	1949	1	26929	29109	0
BAND	276	2	49923	39368	46198
BIBE	4426	1	42466	68667	0
BICA	1079	3	58213	266595	15954
BICY	4009	1	18198	4645	0
BISO	949	1	20812	2228	791
BITH	1029	2	12628	11278	1886751
BLCA	262	2	35446	24146	0
BLRI	1948	1	90411	4984	5305983
BLUE	62	1	1011	0	10550205
BRCA	307	1	45526	19355	0
BUFF	890	2	26065	451	1833311
CACH	752	2	65918	55497	0
CARE	3992	3	56997	42841	734573
CATO	64	1	2331	0	44651
CAVE	360	2	5565	2151	11134
CEBE	47	1	1282	1153	193
CEBR	54	1	3120	197	0
CHAT	214	1	16834	26448	0
CHCU	297	2	35787	26970	3726610
CHIC	109	1	21793	245701	8
CHIR	92	1	70869	68647	0
CHIS	29	1	824	44	6378523
CHOH	761	2	37330	6170	0
CIRO	124	1	33556	1967	5689
COLM	180	2	13906	17798	0
COSW	211	1	1255	0	49644
CRLA	1300	1	34027	18785	0
CRMO	3800	2	33589	32359	0

Table II-1					
Park ID	Park Area (km^2)	Ecoregions	Current Footprint Area	a2a Footprint Area	b2a Footprint Area
CUGA	243	1	7977	2351	0
CURE	458	2	18424	28	0
CUVA	349	2	8603	0	0
DETO	20	1	1668	114150	328558
DEVA	20614	2	86037	97506	33856
DEWA	582	1	25557	3995	0
DINO	1626	2	42387	8546	0
EFMO	42	1	4243	52214	51352
ELMA	857	1	8154	1472	0
EVER	3492	1	10115	9339	0
FLFO	63	1	588	0	0
FLNI	32	1	997	0	1066053
FOBO	22	1	1322	206	87059
FOBU	88	1	8725	0	0
FONE	21	2	1899	0	0
FRSP	187	1	16682	6851	2960057
GARI	157	1	10609	2021	8985019
GETT	86	2	7237	1539	0
GLAC	7455	2	37827	1995	0
GLCA	2051	2	55869	117387	0
GOGA	331	2	5680	3308	0
GOSP	68	1	4135	113822	0
GRBA	557	1	16386	67	2
GRCA	8158	3	91991	60917	1030869
GRKO	27	1	390	0	0
GRPO	40	1	721	0	0
GRSA	825	2	27495	1601	0
GRSM	3455	2	24937	8	0
GRSP	129	1	8665	3056	6894278
GRTE	2247	1	21543	37961	0
GUMO	589	2	13626	230	6179871
HAFO	57	1	1308	117329	0
HOBE	25	1	1975	93447	0
HOCU	38	1	6929	131571	4747055
HOFR	20	1	3190	20071	0
HOSP	66	1	1320	1066357	0
HOVE	31	1	3956	51411	0

Table II-1					
Park ID	Park Area (km^2)	Ecoregions	Current Footprint Area	a2a Footprint Area	b2a Footprint Area
ILMI	2601	2	21880	17928	0
INDU	233	1	20492	57237	0
ISRO	1009	1	8037	1998	0
JELA	162	2	3359	72598	0
JODA	165	2	34816	0	0
JODR	205	1	5965	27173	0
JOTR	4858	2	49443	59	0
KEMO	43	1	1307	54121	0
KEWE	33	1	389	1194	39
KICA	2975	1	27426	711	0
KIMO	42	1	1771	0	10478127
KNRI	30	1	736	620	0
LABE	365	1	3639	0	0
LACH	539	1	7553	14408	0
LAME	9877	2	99527	112707	0
LAMR	391	1	6730	22989	0
LARO	1405	1	30490	6311	0
LAVO	778	1	38242	10975	0
LIBI	21	1	623	391182	0
LIRI	165	1	4839	2721	0
LOWE	21	1	405	303399	0
LYJO	30	1	1858	14	10465018
MACA	396	1	5151	0	0
MANA	58	1	953	35570	0
MEVE	394	1	12792	19191	0
MIMA	30	1	351	216254	0
MNRR	899	2	32966	263895	0
MOJA	9574	1	41439	9022	495978
MONO	27	1	1049	18707	0
MORA	1758	1	35261	4411	0
MORR	37	1	596	13735	0
MORU	23	1	455	0	0
NABR	71	1	2473	3081	0
NACC	36	1	487	116531	0
NACE	131	1	6479	70020	5140590
NATR	1628	3	106447	27299	0
NEPE	99	3	79298	27881	101816

Table II-1					
Park ID	Park Area (km^2)	Ecoregions	Current Footprint Area	a2a Footprint Area	b2a Footprint Area
NERI	647	1	11748	0	0
NIOB	409	1	36897	171369	0
NOCA	3917	1	31276	11246	0
OBRI	167	1	6897	2798	0
OLYM	6636	1	34152	4870	0
ORPI	1814	1	13811	1520	0
OZAR	870	1	27511	31166	0
PAAL	29	1	940	34812	100712
PECO	77	2	1887	3552	6762574
PEFO	1477	1	13899	2855	0
PERI	47	1	1074	0	0
PETE	77	2	2576	1595190	2328
PETR	100	1	2145	699	2396267
PIMA	22	1	1769	3533	0
PINN	220	1	3640	851	0
PIRO	554	1	20550	2	0
PORE	28	1	682	786	1896581
PRWI	106	1	2469	0	718
REDW	602	2	24613	10716	0
RICH	59	1	1595	246318	11467019
ROCR	114	1	4111	4244	991080
ROLA	924	1	28219	14140	1663721
ROMO	1840	1	45731	2127	880379
SAAN	38	1	936	183963	0
SACN	1466	2	86739	175846	0
SAGU	656	2	21297	70830	0
SAMO	651	1	15558	11269	0
SAND	114	1	1911	7457	0
SAPU	28	1	2723	2810	12007813
SARA	42	1	1844	51687	0
SEQU	2382	1	27092	5743	0
SHEN	1151	1	44759	103	0
SHIL	23	1	473	2628270	0
SLBE	529	1	11571	0	0
STRI	25	1	970	810	0
SUCR	33	1	1289	2459	0
TAPR	101	1	4917	67711	0

Table II-1					
Park ID	Park Area (km^2)	Ecoregions	Current Footprint Area	a2a Footprint Area	b2a Footprint Area
THRO	629	1	21785	7405	0
TIMU	139	1	1697	108	0
UPDE	566	2	12082	0	0
VAFO	39	1	2035	254366	0
VICK	33	1	720	14548	2232817
VOYA	1584	1	4592	0	0
WACA	54	2	802	4437	0
WHIS	321	2	19079	13249	0
WHSA	952	1	11166	16550	0
WICA	249	1	43606	18150	0
WICR	26	1	1053	1378	0
WUPA	287	1	4381	121070	0
YELL	15055	2	89755	76989	0
YOSE	4703	1	50230	8084	0
ZION	1028	2	9803	4702	0

Table II-2. Supplemental table of abbreviations and address for each national park.

Park ID	Location
ACAD	Acadia National Park, ME
AGFO	Agate Fossil Beds National Monument, NE
ALFL	Alibates Flint Quarries National Monument, TX
ALPO	Allegheny Portage Railroad National Historic Site, ME
AMIS	Amistad National Recreational Area, TX
APCO	Appomattox Courthouse National Historical Site, VA
APIS	Apostle Islands National Seashore, WI
ARCH	Arches National Park, UT
BADL	Badlands National Park, SD
BAND	Bandelier National Monument, NM
BIBE	Big Bend National Park, TX
BICA	Bighorn Canyon National Recreation Area, MT
BICY	Big Cypress National Preserve, FL
BISO	Big South Fork National River and Recreation Area, TN
BITH	Big Thicket National Preserve, TX
BLCA	Black Canyon of the Gunnison National Park, CO
BLRI	Blue Ridge Parkway, NC
BLUE	Bluestone National Scenic River, WV
BRCA	Bryce Canyon National Park, UT
BUFF	Buffalo National River, AR
CACH	Canyon de Chelly National Monument, AZ
CARE	Capitol Reef National Park, UT
CATO	Catoctin Mountain National Park, MD
CAVE	Carlsbad Caverns National Park, NM
CEBE	Cedar Creek and Belle Grove National Historical Park, VA
CEBR	Cedar Breaks National Monument, UT
CHAT	Chattahoochee River National Recreation Area, GA
CHCU	Chaco Culture National Historical Park, NM
CHIC	Chickasaw National Recreation Area, OK
CHIR	Chiricahua National Monument, AZ
CHIS	Channel Islands National Monument, CA
CHOH	Chesapeake and Ohio Canal National Historical Park, MD

Table II-2	
Park ID	Location
CIRO	City of Rocks National Reserve, ID
COLM	Colorado National Monument, CO
COSW	Congaree National Park, SC
CRLA	Crater Lake National Park, OR
CRMO	Craters of the Moon National Monument and Preserve, ID
CUGA	Cumberland Gap National Historic Park, KY
CURE	Curecanti National Recreation Area, CO
CUVA	Cuyahoga Valley National Park, OH
DETO	Devils Tower National Monument, WY
DEVA	Death Valley National Park, NV
DEWA	Delaware Water Gap National Recreation Area, NJ
DINO	Dinosaur National Monument, CO
EFMO	Effigy Mounds National Monument, IA
ELMA	El Malpais National Monument, NM
EVER	Everglades National Park, FL
FLFO	Florissant Fossil Beds National Monument, CO
FLNI	Flight 93 National Monument, PA
FOBO	Fort Bowie National Historic Site, AZ
FOBU	Fossil Butte National Monument, WY
FONE	Fort Necessity National Battelfield, PA
FRSP	Fredericksburg and Spotsylvania National Military Park, VA
GARI	Gauley River National Recreation Area, WV
GETT	Gettysburg National Military Park, VA
GLAC	Glacier National Park, MT
GLCA	Glen Canyon National Recreation Area, AZ
GOGA	Golden Gate National Recreation Area, CA
GOSP	Golden Spike National Historic Site, UT
GRBA	Great Basin National Park, NV
GRCA	Grand Canyon National Park, AZ
GRKO	Grant-Kohrs Ranch National Historic Site, MT
GRPO	Grand Portage National Monument, MN
GRSA	Great Sand Dunes National Park and Preserve, CO
GRSM	Great Smoky Mountains National Park, TN
GRSP	Green Springs National Historic Landmark District, VA

Table II-2	
Park ID	Location
GRTE	Grand Teton National Park, WY
GUMO	Guadalupe Mountains National Park, TX
HAFO	Hagerman Fossil Beds National Monument, ID
HOBE	Horseshoe Bend National Military Park, AL
HOCU	Hopewell Culture National Historical Park, OH
HOFR	Home of Franklin D. Roosevelt National Historic Site, NY
HOSP	Hot Springs National Park, AR
HOVE	Hovenweep National Monument, CO
ILMI	Illinois and Michigan Canal National Heritage Corridor, IL
INDU	Indiana Dunes National Lakeshore, IN
ISRO	Isle Royale National Park, MN
JELA	Jean Lafitte National Historical Park and Preserve, LA
JODA	John Day Fossil Beds National Monument, OR
JODR	John D. Rockefeller Memorial, WY
JOTR	Joshua Tree National Park, CA
KEMO	Kennesaw Mountain National Battlefield Park, GA
KEWE	Keweenaw National Historical Park, MI
KICA	Kings Canyon National Park, CA
KIMO	Kings Mountain National Military Park, SC
KNRI	Knife River Indian Villages National Historic Site, ND
LABE	Lava Beds National Monument, CA
LACH	Lake Chelan National Recreational Area, WA
LAME	Lake Mead National Recreation Area, NV
LAMR	Lake Merideth National Recreation Area, TX
LARO	Lake Roosevelt National Recreation Area, WA
LAVO	Lassen Volcanic National Park, CA
LIBI	Little Bighorn Battlefield National Monument, SD
LIRI	Little River Canyon National Preserve, AL
LOWE	Lowell National Historical Park, MA
LYJO	Lyndon B. Johnson National Historical Park, TN
MACA	Mammoth Cave National Park, KY
MANA	Manassas National Battlefield Park, VA
MEVE	Mesa Verde National Park, CO
MIMA	Minute Man National Historical Park, MA

Table II-2	
Park ID	Location
MNRR	Missouri River National Recreational Area, MO
MOJA	Mojave National Preserve, CA
MONO	Monocacy National Battlefield, MD
MORA	Mount Ranier National Park, WA
MORR	Morristown National Historical Park, NJ
MORU	Mt. Rushmore National Memorial, SD
NABR	Natural Bridges National Monument, UT
NACC	National Mall and Memorial Parks, DC
NACE	National Capital Parks East, DC
NATR	Natchez Trace Parkway, MS
NEPE	Nez Perce National Historical Park, ID
NERI	New River Gorge National River, WV
NIOB	Niobrara National Scenic River, NE
NOCA	North Cascades National Park, WA
OBRI	Obed Wild and Scenic River, TN
OLYM	Olympic National Park, WA
ORPI	Organ Pipe Cactus National Monument, AZ
OZAR	Ozark National Scenic Riverways, MO
PAAL	Palo Alto Battlefield National Historical Park, TX
PECO	Pecos National Historical park, NM
PEFO	Petrified Forest National Park, AZ
PERI	Pea Ridge National Military Park, AR
PETE	Petersburg National Battlefield, VA
PETR	Petroglyph National Monument, NM
PIMA	Hohokam Pima National Monument, AZ
PINN	Pinnacles National Monument, CA
PIRO	Pictured Rocks National Lakeshore, MI
PORE	Point Reyes National Seashore, CA
PRWI	Prince William Forest Park, VA
REDW	Redwood National Park, CA
RICH	Richmond National Battlefield Park, VA
ROCR	Rock Creek Park, DC
ROLA	Ross Lake National Recreation Area, WA
ROMO	Rocky Mountain National Park, CO

Table II-2	
Park ID	Location
SAAN	San Antonio Missions National Historical Park, TX
SACN	Saint Croix National Scenic Riverway, WI
SAGU	Saguaro National Park, AZ
SAMO	Santa Monica Mountains National Recreation Area, CA
SAND	Sand Creek Massacre National Historic Site, CO
SAPU	Salinas Pueblo Missions National Monument, NM
SARA	Saratoga National Historical Park, NY
SEQU	Sequoia and Kings Canyon National Park, CA
SHEN	Shenandoah National Park, VA
SHIL	Shiloh National Military Park, TN
SLBE	Sleeping Bear Dunes National Lakeshore, MI
STRI	Stones River National Battlefield, TN
SUCR	Sunset Crater Volcano National Monument, AZ
TAPR	Tallgrass Prairie National Preserve, KS
THRO	Theodore Roosevelt National Park, ND
TIMU	Timucuan Ecological and Historic Preserve, FL
UPDE	Upper Delaware Scenic and Recreational River, NY
VAFO	Valley Forge National Historical Park, PA
VICK	Vicksburg National Military Park, MS
VOYA	Voyageurs National Park, MN
WACA	Walnut Canyon National Monument, AZ
WHIS	Whiskeytown National Recreational Area, CA
WHSA	White Sands National Monument, NM
WICA	Wind Cave National Park, SD
WICR	Wilson's Creek National Battlefield, MO
WUPA	Wupatki National Monument, AZ
YELL	Yellowstone National Park, WY
YOSE	Yosemite National Park, CA
ZION	Zion National Park, UT

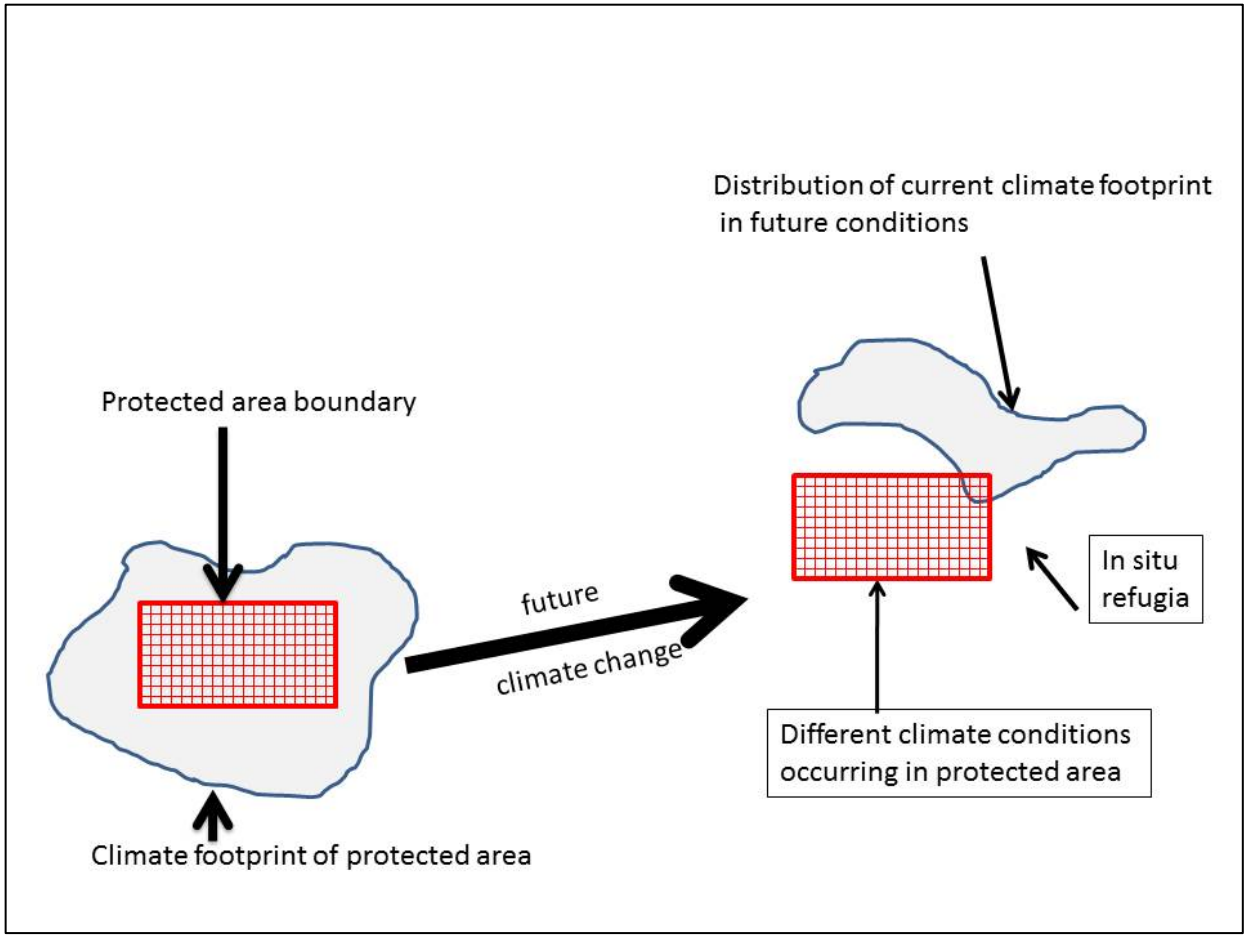

Figure II-1. Climate footprints of protected areas should shift with climate change. The geographic extent of the climate conditions occurring in a protected area under current conditions is a "climate footprint", a measure of the climate similarity of the surrounding landscape. Possible climate footprint dynamics include migrations, expansions, contractions and extinctions. Climate footprints that maintain geographic position during climate change might offer high quality refugia for conservation targets.

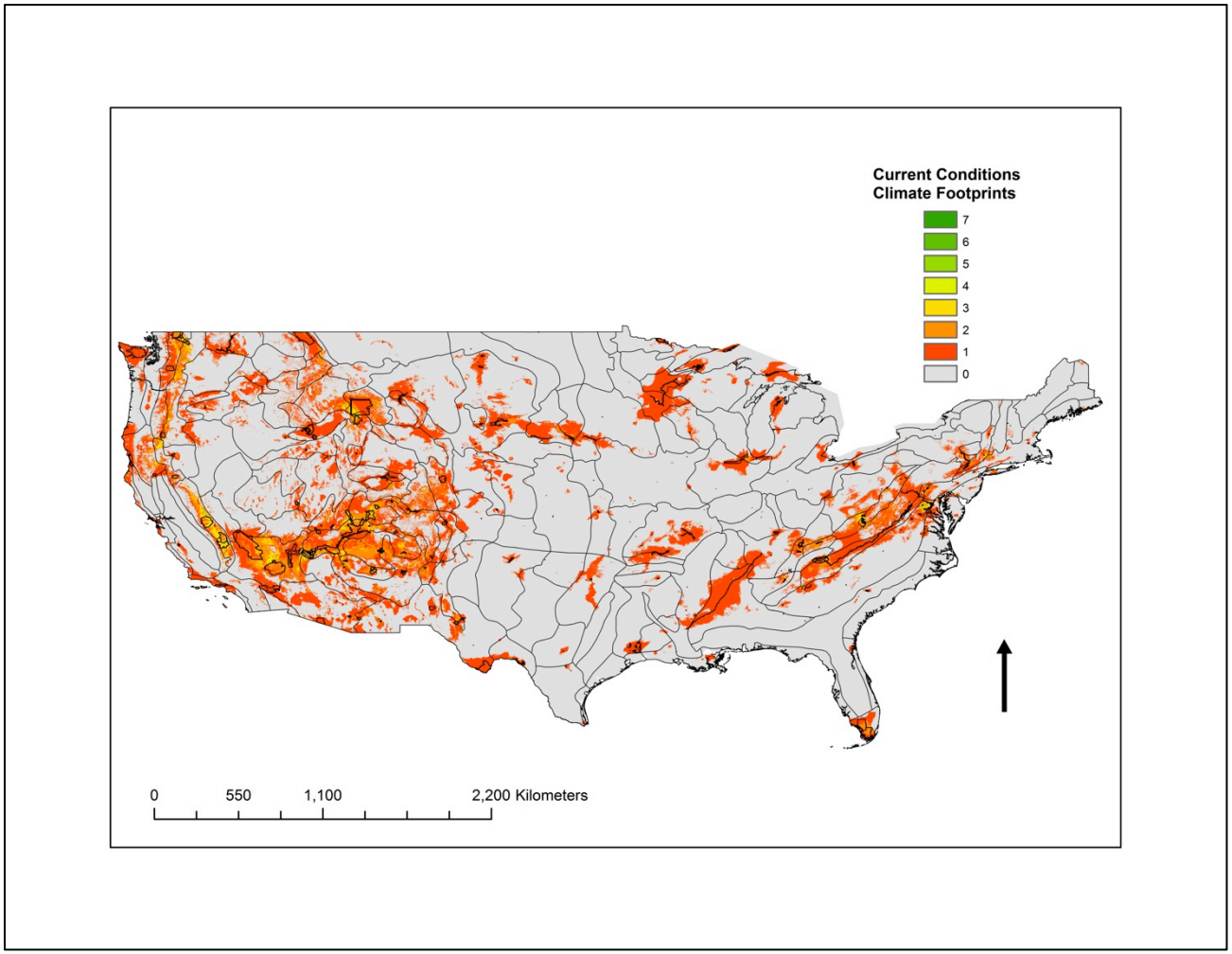

Figure II-2. National Park climate footprints under current conditions. Colors indicate the cumulative number of park climate footprints occupying a map pixel.

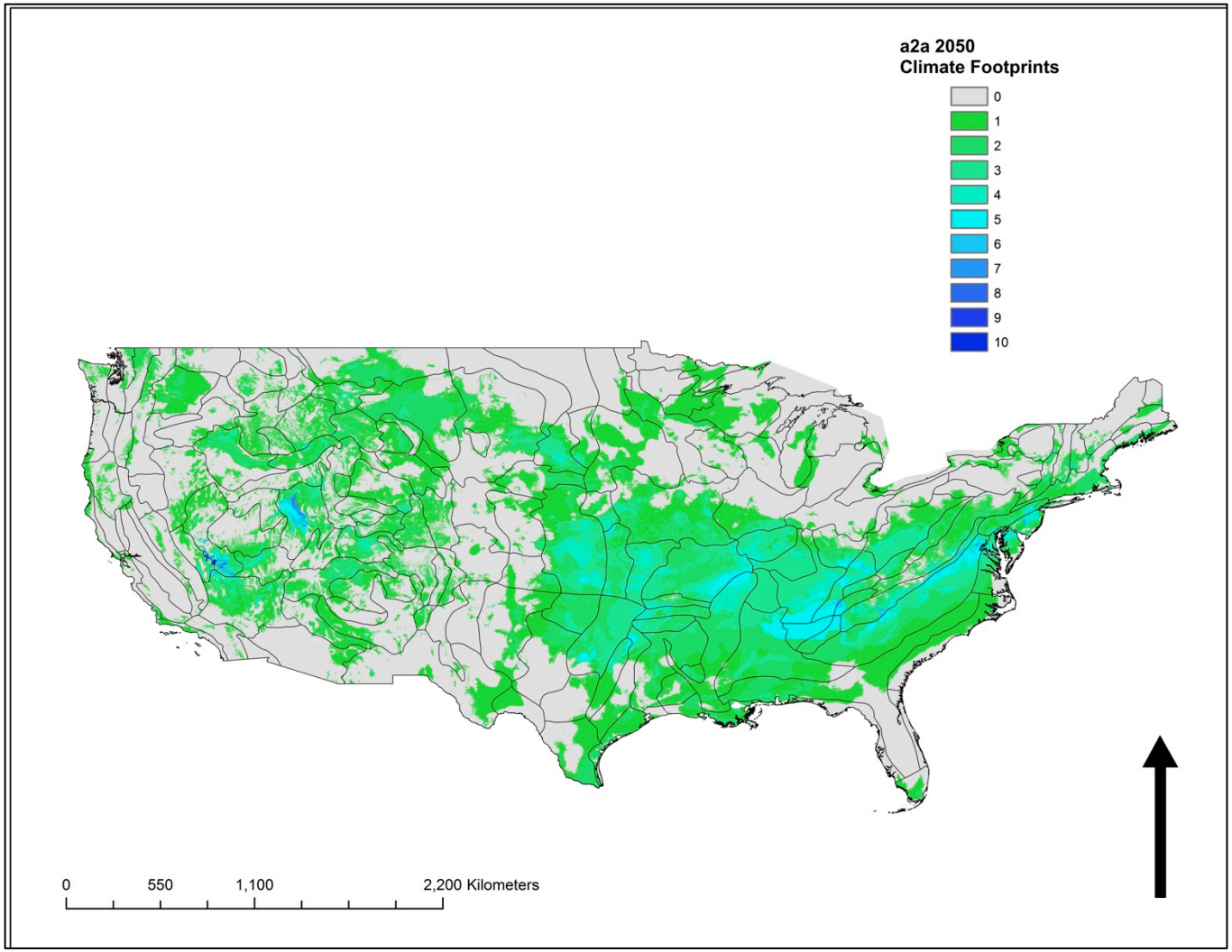

Figure II-3. Accumulation of the current climate footprints of national parks in scenario a2a 2050.

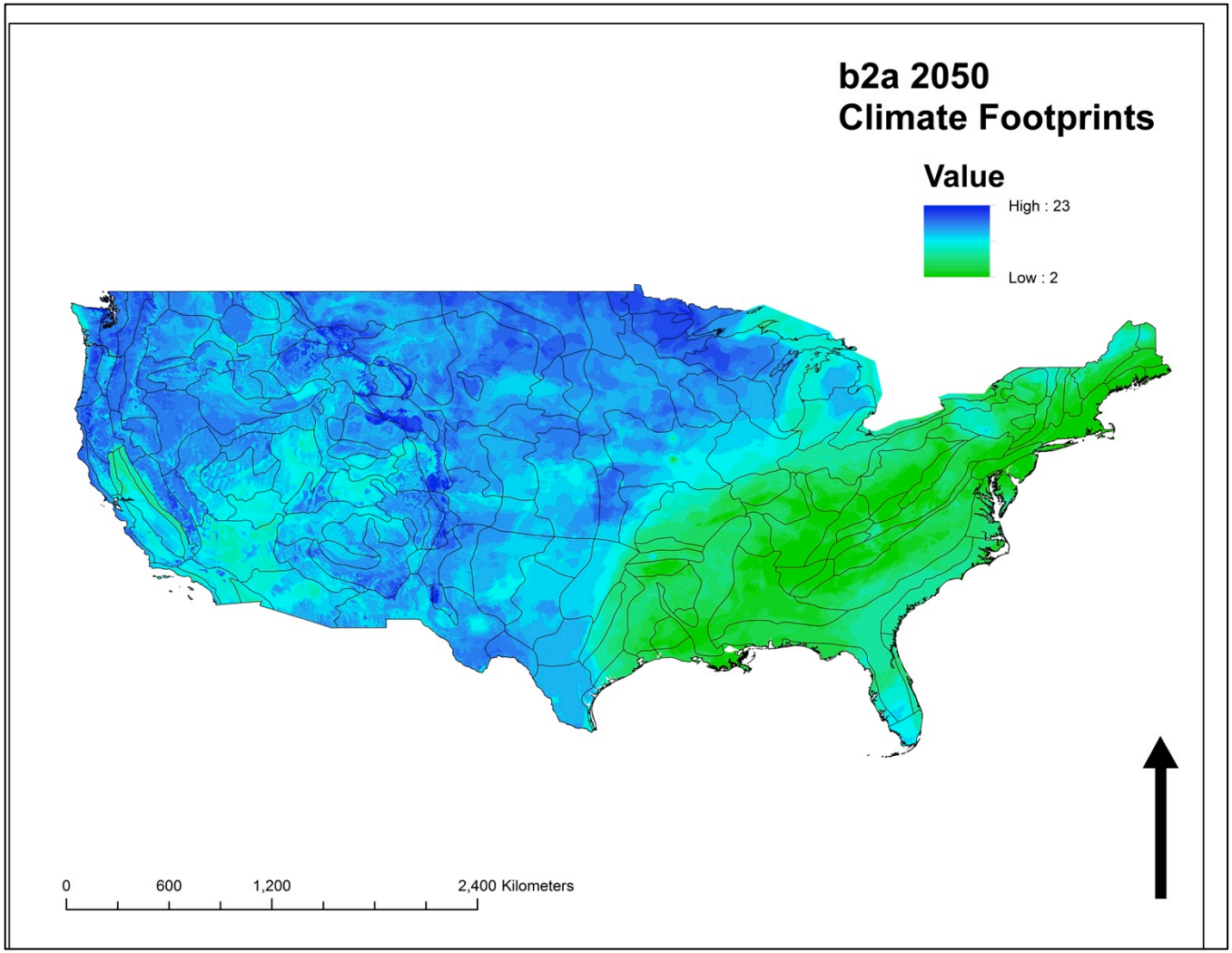

Figure II-4. Accumulation of the current climate footprints of national parks in scenario b2a 2050.

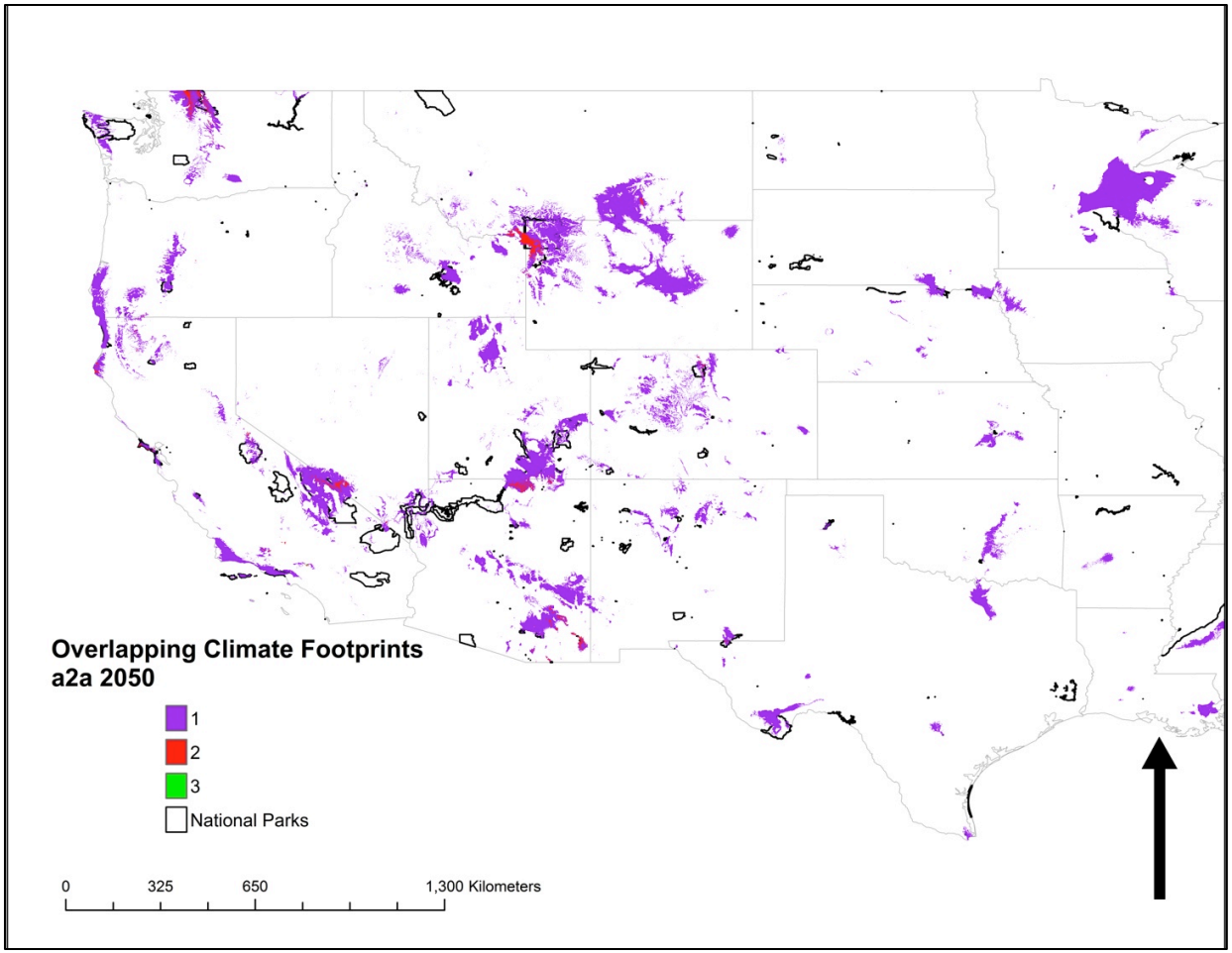

Figure II-5. *In situ* climate refugia (scenario a2a 2050s) in the western United States. The prevalence of large protected areas, in close geographic proximity, maximizes the prospects of demographic connectivity among these parks for plants and animals. Areas with *in situ* climate refugia might offer opportunities to maintain existing ecological configurations in these protected areas.

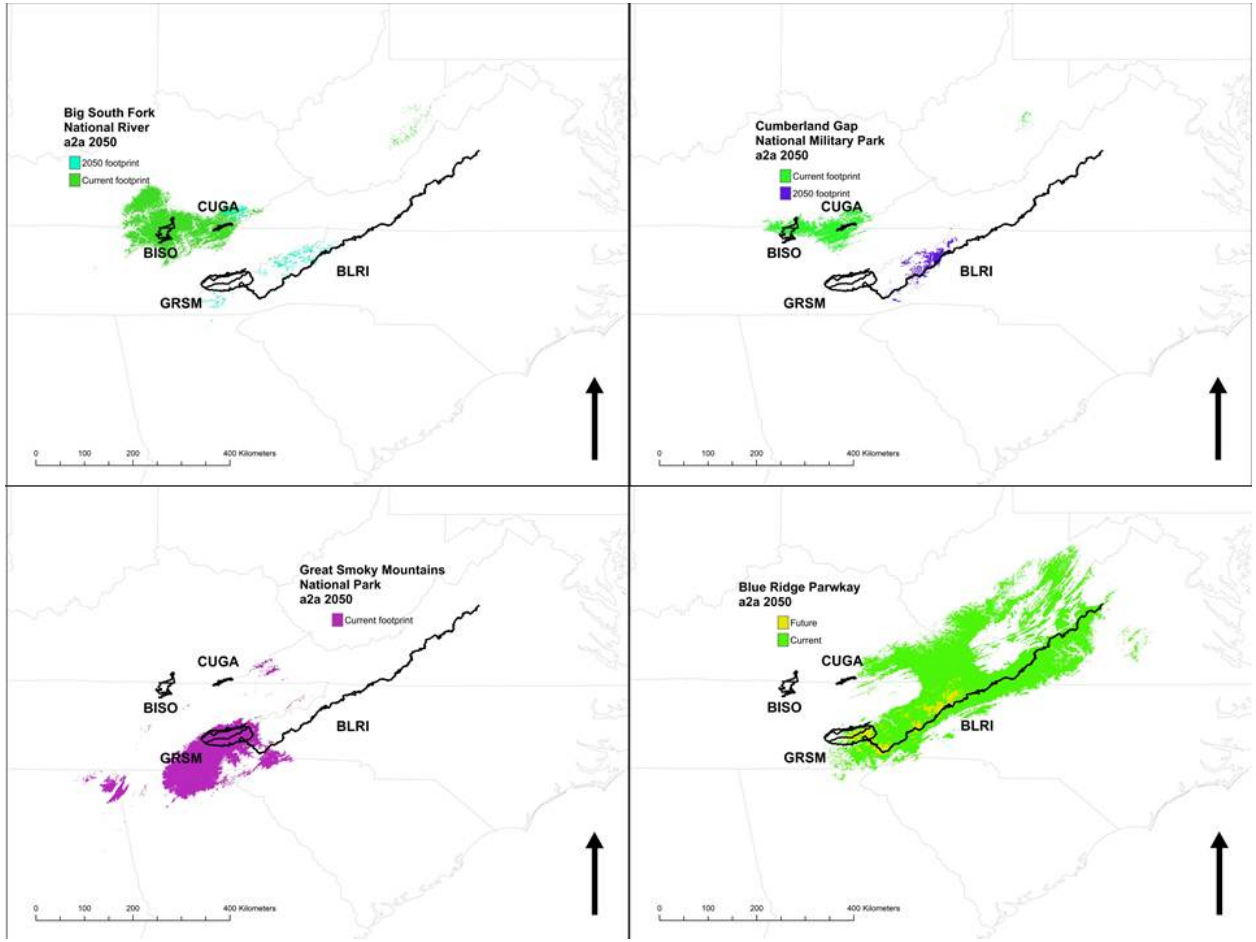

Figure II-6. Climate footprint dynamics of four different protected areas in current and future (a2a 2050) climate scenarios. A-B) Climate footprints migrate to southeast, providing very little *in situ* refugia but remaining in network. C) The climate footprint of the Great Smoky Mountains National Park goes extinct in the future scenario. D) The Blue Ridge Parkway climate footprint contracts in the future scenario but remains *in situ*, accumulates the footprints of parks in panels A and B.

CHAPTER III. PREVALENCE OF IMPERILED AQUATIC INSECT SPECIES IN A HIGH QUALITY PROTECTED AREA NETWORK

This chapter is a slightly modified version of a paper to be submitted for publication.

Robinson, J.L., C.R. Parker, D.A. Etnier and J.A. Fordyce. Prevalence of imperiled aquatic insect species in a high quality protected area network with varying source pools.

Abstract

Protected area networks may be arranged along strong environmental or land use gradients, encompass spatial scales much larger than the range of species occurring within any particular area, or be linked by corridors of varying functional connectivity. In this study I analyze patterns of aquatic insect species diversity across seventeen national parks in the southern highlands of the United States. Species richness of aquatic insects (EPT; orders Ephemeroptera, Plecoptera and Trichoptera) is underestimated by monitoring protocols that consider only immature or larval collections, thus reducing the utility of these data for assessing the rarity or imperilment threats faced by EPT taxa. How this taxonomic bias constraines the quality of conservation assessments generated from benthic data is poorly understood, due to a lack of comprehensive information on the geographic extent of occurrence for most species in the southeast. I sought to bridge this information gap by intensively sampling both immature and adult life history stages of EPTs in aquatic habitats in national parks in two monitoring networks. I relate observed patterns of EPT species diversity to landscape-scale measures of climate similarity and to null models generated from regional species pools estimated from state taxa lists. Park EPT assemblages show differential patterns of the distance decay of similarity among rare to common elements. Our results suggest that EPT assemblages in national parks are not

composed of more rare elements (G1, G2) than would be expected from a random draw of species from the regional source pool, but common elements (G4, G5) are overrepresented relative to the regional species pool. More precise estimates of the geographic range occupied EPT species will be enhanced by collaborative sharing of occurrence records among investigators and by using predictive distribution modeling. In turn, these data can better inform conservation managers how to best prioritize EPT species conservation efforts.

Introduction

Biologists widely recognize that the successful conservation of biodiversity will require the sustained protection of large-scale ecological patterns and processes, above and beyond simple strategies aimed at protecting single species or populations. Gaps in the knowledge of the ecological performance and geographical distributions of species constrain the efficacy of programs directed towards conservation of large taxonomic groups (Cardoso et al. 2011). Protected area networks (PANs) offer opportunities for coordinating resource management for desired ecological endpoints, including intensive surveys of poorly known faunas conducted by expert investigators. In the US National Park Service (NPS), 270 individual parks are organized into 32 different monitoring networks (see http://science.nature.nps.gov/im/networks.cfm) which share biotic and abiotic features and scientific management personnel.

Conservation rankings (e.g., Natureserve 2011) are tools that combine specialist expertise and distribution data to estimate the extinction risk faced by species, across large taxonomic groups and can be organized at state, national and global levels. For poorly understood groups of organisms, estimates of the viability of populations or species are qualified by a great deal of uncertainty regarding the basic distribution and life history of individual species (Cardoso et al. 2010). Since water quality monitoring and benthic surveys of aquatic insect assemblages typically rely upon collections of immature life history stages and morphological taxonomic methods, where individuals may only be identified to family or genus (not species), the vast body of this research cannot aid to

identify imperiled species. Recent advances in molecular taxonomic methods have made species level identifications potentially feasible for biological monitoring (e.g., Zhou et al. 2010). Although these techniques have not yet been widely adopted by researchers to characterize the diversity or composition of benthic communities, Sweeney et al. (2010) provided evidence that these techniques are needed. In that study, experts identified immature EPT specimens, based on morphology, and compared identifications with molecular taxonomic methods. "Taxa richness" metrics, founded on expert identifications of specimens, systematically underestimated the true species richness in benthic samples, as measured by molecular methods. Standard ecological analyses of the results of traditional benthic monitoring methods cannot be related to species-specific distributional or life history knowledge, derived from literature and museum records of adult insects.

A recent interest in community assembly and spatial patterns of beta diversity among stream networks or habitats has great potential for facilitating the broader incorporation of macroecological analyses into stream ecology (Fagan 2002, Grant et al. 2007, Clarke et al. 2008, 2010, Swan and Brown 2011). Implementing this research program will necessarily require species as the appropriate taxonomic unit of study, rather than genera, families or functional feeding groups. To date, most studies of beta diversity in streams have not used data on taxonomic species (but see Finn and Poff (2011) for a great example of this approach using larval chironomids), despite the recognition of the limitations imposed upon biological monitoring by this fundamental knowledge gap (Pond 2010, Sweeney et al. 2010). A baseline understanding of how species distributions are arranged on the landscape is a fundamental component of a robust conservation strategy.

In this study I summarize a multi-year multi-seasonal inventory of EPT species in seventeen national parks in two different monitoring networks distributed across the southern highlands, a hotspot of biological diversity for aquatic organisms (Lydeard and Mayden 1995, Morse et al. 1993, 1997). To evaluate the conservation significance of aquatic insect assemblages in national parks, I compare observed occurrence patterns of EPT species in three categories of perceived threat. I measure turnover among aquatic insect species along geographic and climatic gradients that differentiate between parks, and compare patterns of species turnover among species grouped by perceived extinction risk. I use a null model to ask whether national parks differentially protect aquatic insect species under varying levels of perceived threats.

Methods

Occurrence Data and Species Pools

Over a three year period I, along with Chuck Parker and multiple field assistants, sampled aquatic insect communities from lentic, lotic, and madicolous habitats in sixteen southeastern national parks (Figure 1). Data from previous studies in a seventeenth park (Great Smoky Mountains National Park (NC/ TN) were included in our analyses, but we did not systematically sample that park for this study and relied on previous results for species occurrences (Parker et al. 2007). I obtained global conservation rankings for EPT species using NatureServe Explorer, where species are ranked on a spectrum of very rare (G1) to

very common (G5) (NatureServe 2011). Species without NatureServe rankings (typically recently described species) we conservatively assigned a rank of G5.

We collected immature forms of aquatic insects by hand, kick nets and seines. Adult insects were collected with black lights, beat sheets, aerial nets, and by rearing live larvae and pupae in the laboratory via the metamorphotype method (Etnier et al. 2010). We located sampling locations from maps, prior collections, Park Service staff, literature records and during exploration of the parks by the investigators. We identified specimens to species whenever possible, relying on the expertise of outside taxonomic experts for some Plecoptera and Ephemeroptera identifications (BK, ED, LJ; see acknowledgments). Some species records we obtained from a DNA barcoding program that associated sequences from immature specimens with sequences from confirmed adult identifications (Zhou et al. 2011). Our sampling efforts were designed as an attempt to census all species present in each; larger parks with more habitats were necessarily sampled more frequently and intensely than parks with few habitats. In this paper I analyze patterns of species presence-absence among individual parks based on the cumulative number of species observed during the course of this study.

Regional species pools were constructed for each state by searching literature and occurrence databases for presence records and consultation with experts (Table S1). I relied heavily upon the North American Plecoptera list (Stark et al. 2009) and a recent review of mayfly records in the southeastern US (McCafferty et al. 2010), supplementing with our own collection records when necessary. Trichoptera records are derived from

published reviews (Frazer et al. 1991, Harris et al. 1991, Harris et al. 1996, Etnier et al. 1998, Flint et al. 2004, 2008, 2009, Lenat et al. 2010, Floyd et al. in press) and scattered literature records compiled by CRP and JLR. Regional analyses are useful for this application but I should note that species specific estimates of the occupied geographic range are not available for most EPT taxa.

Spatial and climatic dissimilarity

Using a GIS, I found the geographic centroid of each national park and state. I then used *R* (*fields* package, v. 6.6.3, Furrer et al. 2012) to compute all pairwise great circle distances between park and state centroids, respectively. To analyze climatic differences among parks, I used downscaled bioclimatic variables from WORLDCLIM (Hijmans 2005). For all 1 km^2 raster cells at least partially occupied by a park I extracted annual mean temperature, mean diurnal temperature range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, and precipitation of the driest month variables. I used principal components analysis to summarize the variation among parks and calculated a mean score for each park along each principal component axis. I then used these PCA scores to calculate the pairwise Euclidean climate distance between all parks along all PCA axes to generate a pairwise dissimilarity matrix.

Community dissimilarity and beta diversity

Species occurrence data for parks and states were summarized in presence-absence matrices. Using *R* package *vegan* (v. 2.0-2, Oksanen et al. 2011), I calculated pairwise

community Jaccard dissimilarities among parks and states. Since some parks did not have records with confirmed species level identifications for some insect orders, I removed these parks from pairwise distance measures (Ephemeroptera: RUCA, Plecoptera: FODO, STRI). To measure and compare beta diversity among groups of taxa, I tested for distance-decay relationships (DDRs) by regressing dissimilarity measures onto geographic and climate distances, then testing whether the slopes of regression lines were significantly different from zero.

The aquatic insect fauna of the Great Smoky Mountains National Park is particularly well studied and prior records have previously been compiled for all three orders of aquatic insects considered here (Parker et al. 2007). Although this park is several orders of magnitude larger than other parks in this study, the GRSM has been the target of far more sampling effort than any other park in our three year study (Fig. 2d) and has higher species richness (for all 3 orders) than any of the sixteen parks in our survey. To evaluate the effect of this sampling bias in our analyses, I removed GRSM records, recalculated pairwise community dissimilarities and tested for DDRs on the reduced dataset. To test whether EPT species under varying levels of perceived risk exhibit differential patterns of beta diversity among parks, I grouped species into 3 categories of NatureServe rankings (G1 and G2, G3 and G4, G5), then tested for distance-decay of similarity.

Null models of regional species pools

National parks, with greater restrictions on permitted activities than many natural areas, might differentially protect rare habitats or populations of imperiled species.

Particularly, since the locations of many parks are designed to protect historical interests and not necessarily the biodiversity of aquatic insects, parks might systematically over or under protect rare or common species. To test the hypothesis that national park EPT assemblages have more rare members than a random sample of the regional species pool, (for each park) I used a null model to draw 99,999 null assemblages from each park-specific regional species pool. Each of these null assemblages had the same species richness as observed within the park, but with a random distribution of G1-G5 values. For each observed park EPT assemblage, for each category of rarity (G1-G5), I calculated a p-value for the observed frequency of species in each category of rarity, based on the 100,000 total observations.

Results

Patterns of species richness

Observed richness of EPT species varied by two orders of magnitude among parks; all insect orders exhibited strong species-area relationships among parks (Fig. 2a-c; data inTable S2). This relationship was strongly driven by the Great Smoky Mountains National Park (GRSM), which has been sampled far more intensively despite having a total area nearly 10 times larger than any other park in our study (Figure 2d; Table 1). Omitting species records from GRSM from analyses (Table S3) reduced the slope of Ephemeroptera and Plecoptera species-area regressions, but increased the slope of Trichoptera species-area regression, implying that species richness of Trichoptera may be saturated at larger areas. EPT species richness shows no species-area relationship among states; no

parameter estimates were significantly different from zero. Park species richness was not related to estimated regional species pool richness for any of the three insect orders.

Distance decay of climatic and EPT assemblage similarity among parks

Principal component analysis of climate patterns within parks revealed that parks are distributed along a strong precipitation gradient: the first principal component axis most heavily weighted precipitation variables and accounted for 98.4% of the variance among parks (Table S4). Ordination of parks on principal component axes calculated without annual precipitation data yielded similar results (Figure S1) but explained less cumulative variance among parks than analyses which included annual precipitation and were omitted from the remaining analyses. A significant distance decay of climate similarity was observed among all parks ($F_{1, 134}$ = 8.306, p = 0.005, r^2= 0.051, slope = 0.137); omitting the large and environmentally heterogeneous GRSM increased the slope and improved the fit of this regression ($F_{1, 118}$ = 21.030, p < 0.001, r^2= 0.144, slope = 0.298). Strong DDR relationships were detected across southeastern states for all three aquatic insect orders (Table 2). Considering only the states where surveyed parks are located diminished the strength and statistical significance of this relationship, for Ephemeroptera the relationship disappeared entirely.

Among park assemblages, DDRs were detected in Plecoptera and Trichoptera, but not Ephemeroptera. After removing GRSM from analyses, distance-decay in Trichoptera assemblages was not quite statistically significant but remained so for Plecoptera. Regressions of assemblage dissimilarities onto climate distances yielded contrasting

results; no DDR was detected among Plecoptera assemblages using all parks, but all three insect orders had significant distance decay when GRSM was excluded. Species assemblages containing members ranked as" least imperiled" (G5) showed no significant DDR among parks, but the similarity more imperiled assemblages did decay with geographic distance (Table 3). Partial mantel test results indicate that changes in pairwise aquatic insect assemblage dissimilarity were correlated with geographic distance, after correcting for spatial autocorrelation in temperature and precipitation (Table 4).

Null model assembly of faunal composition from regional source pools

The resampling procedure provided, for each aquatic insect order, a null distribution of assemblages where the composition of rarity is determined by random draw from the species pool. (Table 5). This allows estimation of whether parks have significantly disproportionate occurrences of rare elements. In general, across all three taxonomic orders of aquatic insects considered here, parks disproportionately protect common species. All parks had lower frequencies of occurrence of EPT species ranked G1-G3. Two parks, GRSM and LIRI, had significantly more G4 Plecoptera species than the average random draw from the species pool (p= 0.02 and p=0.009 respectively), but no parks differentially protected G4s. Many parks over protected G5 taxa (Ephemeroptera: 9 parks p<=0.1, Plecoptera: 5 parks p<=0.1, Trichoptera: all parks $p<0.08$).

Discussion

The highland regions of the southeastern United States are widely understood to harbor a significant reserve of insect diversity (Allen 1990). Explanations offered for this pattern have generally assumed that current ranges reflect historical dynamics associated (at least in part) with dispersal from historical glacial refugia (Ross 1953, 1956, 1965, Ross and Ricker 1971, McCafferty 1977, Allen 1990, Hamilton and Morse 1990). Yet, interactions with contemporary environmental heterogeneity are also known to be important drivers of spatial patterns of aquatic insect diversity (Wallace and Merritt 1980, Ward and Stanford 1982, Vinson and Hawkins 1998). Our description of the patterns of species richness across southeastern states, for all three orders, are consistent with the hypothesis that the southern mountains have higher species richness than outlying areas, but a more specific test will require more precise delineations of species ranges within the region.

Here I demonstrate that national parks do not differentially protect rare aquatic insect species, but do over protect common species. Water quality monitoring strategies using macroinvertebrates are premised on the notion that optimum values of ecosystem integrity or condition are at high values of aquatic insect richness, yet in this study areas with high values of aquatic insect richness are not more populated by rare species. These results might be expected from some of these parks, which are historical sites or battlegrounds and not particularly significant in terms of aquatic resources. Yet large, high quality parks such as Great Smoky Mountains National Park, or Mammoth Cave National

Park, have the same pattern of overprotection of common species, as do parks with lower quality resources. I cannot distinguish between the hypothesis that rare species are present at abundances below the limit of detection of our methods, and the hypothesis that rare species populations are aggregated in habitats or systems where there are no national parks (i.e., not in the potential source pool of EPT species for that park).

The importance of range-wide occurrence data for planning conservation strategies

Describing the distribution of rare species is an exercise in inference from small sample size. A fundamental limitation to species-specific conservation efforts is the availability of occurrence records, particularly for insects and other arthropods (Cardoso et al. 2010). This problem may be manifest in at least three different ways: records may not exist, records may not be shared among researchers, or available records may not cover the entire geographic range of a species. Relatively recent developments in predictive modeling of species distributions have facilitated the estimation of species ranges from small numbers of occurrence records (e.g., Phillips et al. 2006, Pearson et al. 2007), but these methods are only now beginning to be used to describe EPT species ranges across North America. The paucity of available, verified collection records of adult specimens of EPT species, in general, combined with the scattered geographic coverage of intense sampling across the region, raises doubts about whether assessments of the rarity or imperilment of species can reasonably be indexed by the number of known occurrence records. Our survey efforts were the first systematic inventory of EPT species richness

attempted in several parks in this study; despite ongoing benthic macroinvertebrate biological monitoring programs.

During the course of this project we collected several species identified in Morse et al. (1993, 1997) as "rare and vulnerable to extirpation" based on small numbers of collection records. For instance, that study suggested that the baetid mayfly *Callibaetis pretiosus* Banks is rare and vulnerable to extirpation, but in this study we collected this species in three different states in very different habitats, suggesting that this species may simply be undercollected or misidentified in collections. Similarly, Morse et al. (1993) suggest that the glossosomatid caddisfly *Agapetus vireo* Ross may be extinct, since at that time those authors had no collection records more recent than the 1940s. We (JLR and CRP) have collected this species at multiple localities along Lookout Mountain and the Cumberland Plateau in AL, GA and TN (see additional records and discussion in Etnier et al. 2010). The leptocerid caddisfly *Ceraclea joannae* Morse and Lenat was previously thought to be endemic to the Little River area of Montgomery Co., NC (Morse and Lenat 2005, NCNHP 2010); in this study we discovered a population of this species in the Obed River (Morgan Co., TN) nearly 350 miles away. Further collection efforts are likely to discover more populations of this species and other putative endemics.

Some aquatic insect species may elude detection even after many decades of intense collecting efforts: in GRSM, new species occurrence records (and indeed, discoveries of undescribed EPT species) continue to be reported (CRP, *pers. comm*), suggesting that even in this well-sampled park the EPT assemblage has not yet been sampled to completion.

The hydropsychid caddisfly *Oropsyche howellae* Ross is one possible (frustrating) example of an undetected species in this park. Despite the intensity of EPT sampling in GRSM, this species has yet to be verifiably reported from within the park (a previous record identified as this species in Morse et al. 1997 we found to be a female of a species of *Diplectrona*; JLR). The only known records of *O. howellae* are from three counties in WNC, all of which border GRSM. The larva of this elusive species continues to evade discovery despite decades of intense investigation at known collection localities and several false positives (Wiggins 1977; Weaver 1985; Huryn 1989).

Similarly, *Rhyacophila accola* Flint was previously known only from two collections in GRSM, one the type series. In our study we collected adults of this species nearly 90 miles away at two sites on the Blue Ridge Parkway in Buncombe Co., NC and one site near Chattooga River (Macon Co., NC), syntopically with an undescribed species of *Agapetus* (since described as *Agapetus flinti* Etnier, Parker and Baxter). These two species provide an interesting contrast: since the 1940s *O. howellae* has been collected ~ 25 times in a small area of perhaps 100 square miles, but not during this study and not along the Blue Ridge Parkway. To our knowledge, *R. accola* has been collected from only five sites, including the type series (1972), three of those collections occurred during the course of this study. Little to nothing is known about the biology or life history of either species, save the collection locality, yet Natureserve ranks *O. howellae* as G2 and *R. accola* as G1.

As a final example, the hydropsychid caddisfly *Diplectrona marianae* Reeves was previously known only from the type locality, a small surface seep and subterranean

stream on Lookout Mountain in Dade Co., GA (Reeves and Paysen 1999). This species is currently ranked G1 by NatureServe. However, during the course of our survey of southeastern national parks, specimens of *Diplectrona marianae* were discovered at the University of Tennessee (in the David A. Etnier Trichoptera Collection) which had been collected (and subsequently misidentified as a species of *Homoplectra*) from several sites along the Cumberland Plateau in White and Franklin counties Tennessee during the 1970s. Subsequently, adult males were collected in a cave passage in Marion Co. TN (Harvey et al. 2012) and several larval specimens collected in Hamilton Co. TN. Larval specimen records of *D. marianae* have now been verified from four TN counties, a distance of almost 100 miles from the type locality.

Determining objective estimates of the threats facing species that are this poorly known will continue to be a challenge for conservation managers. I raise these issues not to unduly criticize previous efforts to assess the imperilment of unique aquatic insect faunas, and not to suggest that there are no imperiled aquatic insect species, but to emphasize that the quantity of occurrence records is not an unbiased estimate of the imperilment risk faced by a particular species. These are a few examples of instances where additional collecting (or re-identification of previously collected specimens) has demonstrated that putatively rare EPT species are more common (or occupy a larger geographic range) than previously believed. Properly qualified, EPT species occurrence records can provide robust evidence of range size contraction or expansion across smaller geographic areas (e.g., DeWalt et al. 2005), but few datasets of this scope and taxonomic quality exist. Rigorous analyses of the rarity or viability of EPT species should consider the

size and rate of occupancy of the full geographic range of target taxa as criteria of imperilment.

Quality of estimates of regional source pools

Our analysis of how parks function to capture aquatic insect species diversity (from the regional source pool) uses source pools derived from lists of species occurring in each state. Whether a species is distributed across an entire state, or only in certain regions of the state, is a question which the available distributional data simply cannot answer. This lack of information has in fact motivated this dissertation, but it might be instructive to examine how changes in the source pools we assigned to parks might influence these results and to justify why we selected this spatial grain for source pools.

We did not detect a distance-decay of similarity relationship among EPT assemblages in the study states (Table 2), but species richness does vary among states (Table 8). To the extent that species are restricted to certain areas of states (e.g., coastal plains or mountains) these source pools may over predict local species richness. However, to the extent that the proportion of rare species in the local source pool stays constant with grain size, our results should not be affected by using smaller source pools. This may not always be a reasonable assumption, since certain areas may have rare species in higher frequency of occurrence than other areas, but those data are simply not available. Certainly species occurrences aggregate at some spatial grains but the frequency of occurrence of various imperilment categories are similar among parks and states, with G1s always fewer than G2s, etc. (Table 6, 8).

Similarly, considering larger source pools of species cannot provide more confidence in our null model results. It is true that G1s are rare by definition (and in our data, see Table 7 and 9), so adding members to the source pool will not increase the probability of drawing G1s in null assemblages unless G1s are added at a greater frequency than other categories are added. For example, consider that since TN and KY are adjacent, species found in Kentucky might possibly be found in Obed River (Morgan Co., TN) and therefore we include KY species in the source pool for this park. As a result, we have added very many G5s and very few G1s to our source pool, and the chance of drawing more G1s from this pool becomes even slimmer than when we used TN alone.

Every estimate of the "regional source pool" is an abstraction, and there are advantages to considering different possible forms of the pool. In this analysis, the question I set out to answer was "Do parks differentially protect rare or common species"? The best available estimate of the potential colonizers of a park remains published lists of species occurring in that state, despite the potential advantages of other hypothetical sources of these data. An optimal source pool for a park would be compiled from range maps or predictions based on occurrence data, but very few state lists include this information and locality data are scattered throughout the literature, rarely compiled in this format. Compiling occurrence records of EPT species across eastern North America is an active area of my current research efforts.

Effect of regional source pools on beta diversity among PANs

Change in faunal assemblages is an expected result when sites are distributed along strong environmental gradients or when sites occupy different potential source pools of colonizers. In this study, I have shown that a substantial amount of faunal turnover among national parks occurring in southeastern states is a function of variation in the regional species source pool. Among the parks we sampled in our study, rare (G1 and G2) species show much greater turnover among parks than do more common widespread species, and that parks that are in closer geographic proximity generally have more similar species assemblages (even after correcting for differences in temperature and precipitation patterns among parks).

Regionally, EPT assemblages exhibit distance decay of similarities among all southeastern states (including those states which are outside of the Appalachian uplift), but these patterns were not detected among our study states alone. This seemingly paradoxical result might be explained if EPT gamma diversity is greatest in the core mountainous region shared by these states, decreasing with distance away from the mountains (see Figure 1). The relatively high species richness of EPT taxa observed from BLRI and GRSM is consistent with this explanation, but without more refined range estimates for each EPT species I cannot yet definitively test this hypothesis. This is an active area of my research, but requires the compilation of records from many institutions and individuals across North America.

It is important to consider that national parks are not the only PANs in the southeastern US; many other state, federal and NGO entities administer lands managed for conservation objectives. Thus, our analysis cannot be construed as an assessment of the adequacy of imperilment designations for EPT taxa in general, although I do provide evidence that some species are less rare or range restricted than previously considered. Vast holdings of national forests across the southeastern US are likely (in sum) to capture a larger fraction of regional aquatic insect biodiversity than the relatively tiny network of national parks, but these lands experience many different types of land use and do not all share the high level of protection afforded to the PANs I consider here. Given these observed patterns of occurrence and rarity, it is certain that some rare species (or species we did not collect within these PANs) occupy localities across these additional lands. Since a substantial number of EPT species are known from a small handful of localities or collection events, more research is needed to determine whether these patterns in regional species richness are driven by variation in sampling effort or truly reflect narrow geographic extents of occurrence. Integrating adult sampling techniques, museum data and literature occurrence records with spatial analyses, to derive estimates of the geographic range of species, should speedily facilitate the answering of these questions and the effective conservation of EPTs across protected area networks and beyond.

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APPENDIX III. FIGURES AND TABLES.

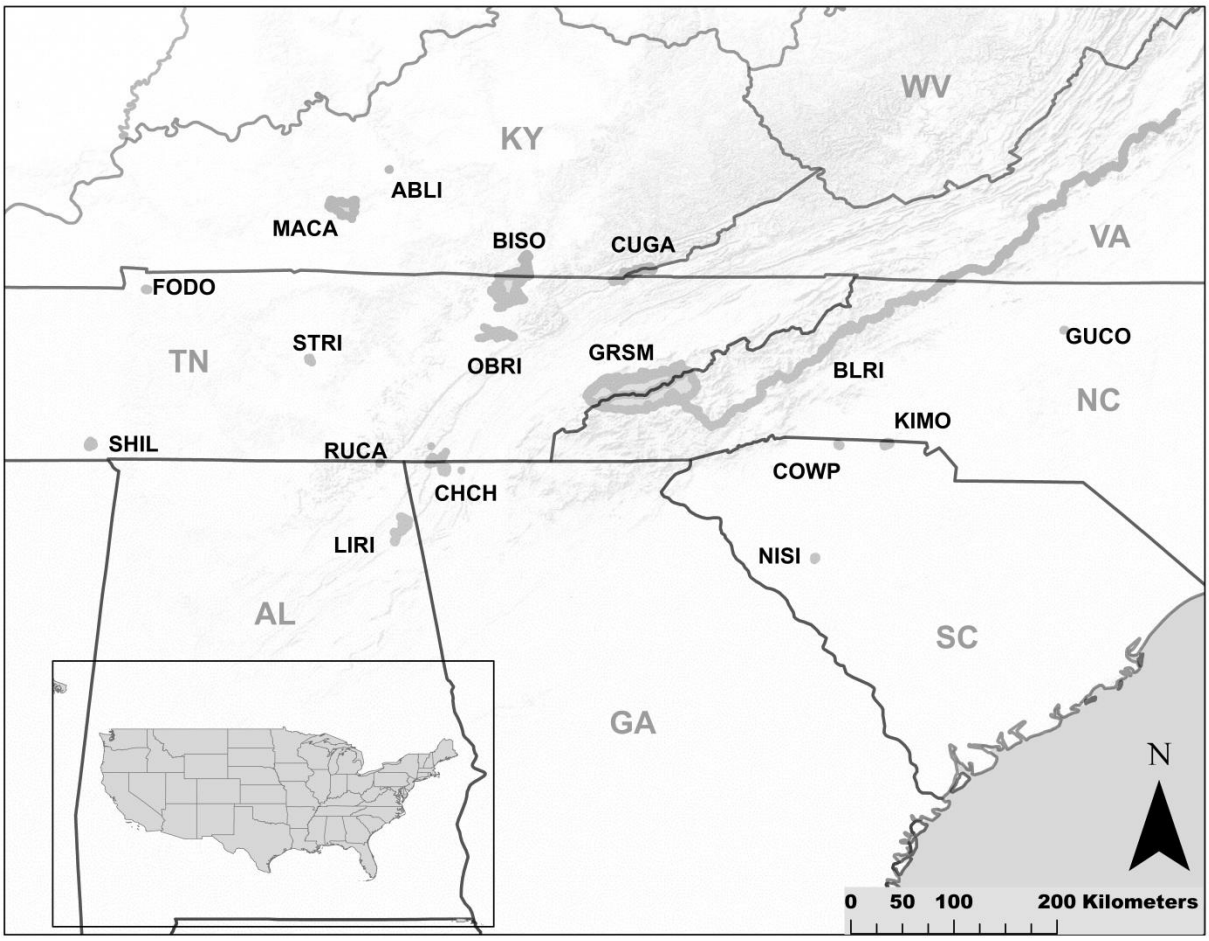

Figure III-1. Location of the 17 US National Parks sampled in this study. ABLI= Abraham Lincoln Boyhood Home (Hodgenville, KY), BISO= Big South Fork National River and Recreation Area (Oneida, TN), BLRI= Blue Ridge Parkway (Asheville, NC), CHCH= Chickamauga and Chattanooga National Military Park (Fort Oglethorpe, GA), COWP= Cowpens National Battlefield (Gaffney, SC), CUGA= Cumberland Gap National Historic Park (Middlesboro, KY), FODO= Fort Donelson National Battlefield (Dover, TN), GRSM (Great Smoky Mountains National Park (Gatlinburg, TN), GUCO= Guilford Courthouse National Military Park (Greensboro, NC), KIMO= Kings Mountain National Military Park (Blacksburg, SC), LIRI= Little River Canyon National Preserve (Fort Payne, AL), MACA= Mammoth Cave National Park (Mammoth Cave, KY), NISI= Ninety Six National Historic Site (Ninety Six, SC), OBRI= Obed Wild and Scenic River (Wartburg, TN), RUCA= Russell Cave National Monument (Bridgeport, AL), SHIL= Shiloh National Military Park (Shiloh, TN), STRI= Stone's River National Battlefield (Murfreesboro, TN).

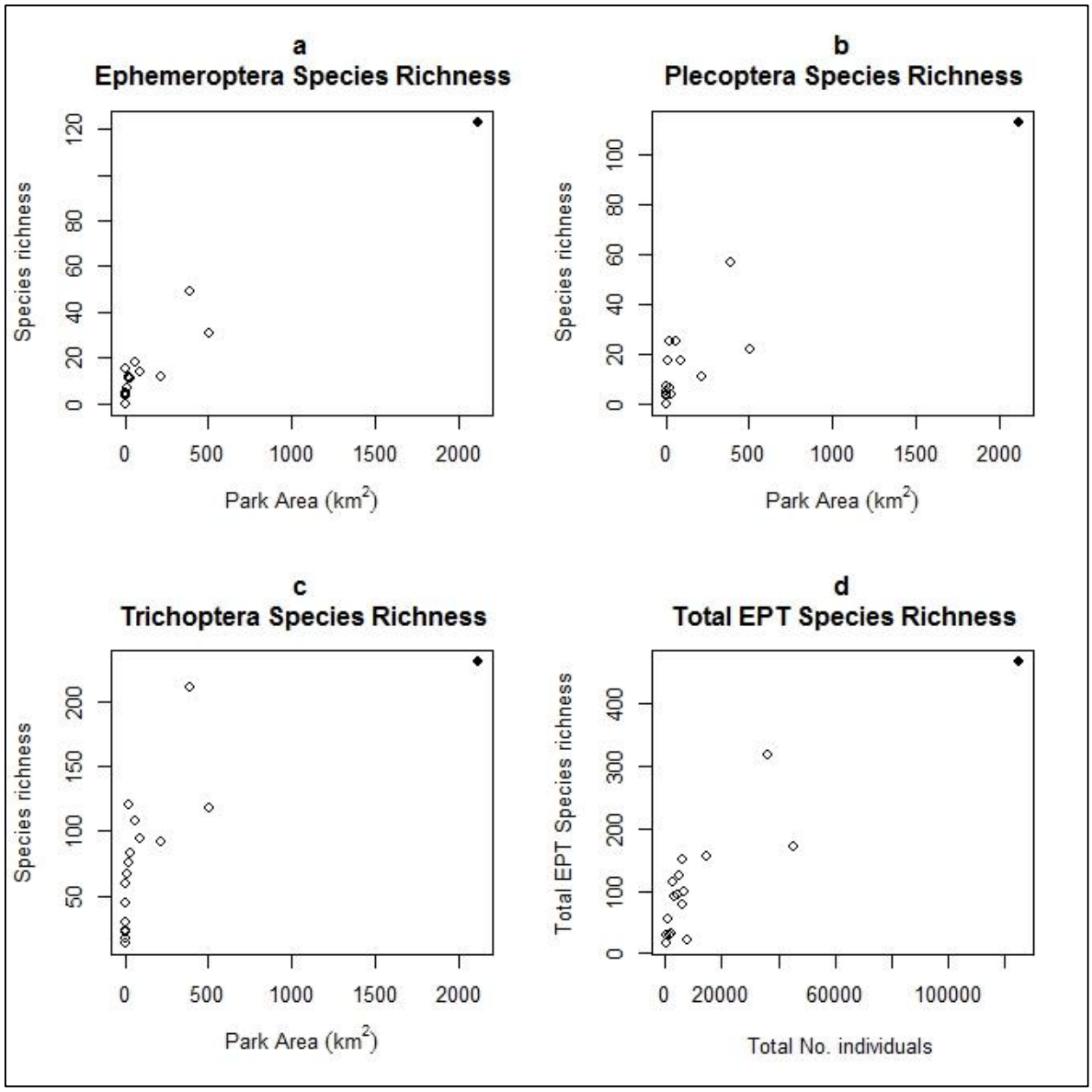

Figure III-2. 2a-c Species richness of EPT orders in 17 national parks, plotted against the park area (km^2). 2d is total EPT species richness plotted against total number of individual insects collected in each park. For all plots, the dark symbol is the heavily sampled Great Smoky Mountains National Park (GRSM).

Table III-1. Parameter estimates for species-area relationships among three insect orders. Omitting GRSM alters slope, strength of relationship. States show no significant species-area relationship.

		Ephemeroptera	Plecoptera	Trichoptera
17 Parks	Slope	2.4	2.2	4.7
	p	6.25E-09	2.78E-07	9.00E-06
	r^2	0.89	0.83	0.72
	F (df)	136.4(1,15)	76.7(1,15)	43.1(1,15)
No GRSM	Slope	1.5	1.4	6.2
	p	7.16E-05	7.15E-03	1.72E-04
	r^2	0.69	0.42	0.62
	F (df)	32.6(1,13)	10.5(1,12)	25.7(1,14)
States	Slope	-0.2	-0.5	-0.3
	p	0.62	0.12	0.73
	r^2	-0.07	0.15	-0.09
	F (df)	0.27(1,10)	2.9(1,10)	0.1(1,10)

Table III-2. Distance-decay regression estimates for southeastern aquatic insect assemblages. Bold font denotes slope estimates significantly different from zero (*=significant at p<0.1, **= significant at p<0.05, *** =significant at p<0.001).

		Slope	*r*	F
Southeastern states	Ephemeroptera	2.93E-04***	0.36	37.78 (1, 64)
	Plecoptera	2.67E-04***	0.43	48.94 (1, 64)
	Trichoptera	2.43E-06***	0.4	43.79 (1, 64)
Study states	Ephemeroptera	1.51E-04	0.06	2.49 (1, 19)
	Plecoptera	1.85E-04	0.14	4.2 (1, 19)
	Trichoptera	2.18E-04	0.1	3.21 (1, 19)
All parks	Ephemeroptera	7.48E-05	-0	0.59 (1, 118)
	Plecoptera	1.15E-04**	0.04	5.19 (1, 103)
	Trichoptera	1.29E-04**	0.03	5.42 (1, 134)
Parks (No GRSM)	Ephemeroptera	1.04E-04	0	1.35 (1, 103)
	Plecoptera	1.69E-04**	0.03	4.06 (1, 89)
	Trichoptera	1.75E-04*	0.02	3.89 (1, 118)
Climate (Temp/Precip)	Ephemeroptera	4.72E-04***	0.15	21.92 (1, 118)
	Plecoptera	1.39E-05	0.01	2.68 (1, 103)
	Trichoptera	3.06E-04**	0.06	10.11 (1, 134)
Climate (No GRSM)	Ephemeroptera	3.34E-04**	0.06	7.53 (1, 103)
	Plecoptera	2.13E-04**	0.04	4.46 (1, 89)
	Trichoptera	3.60E-04**	0.07	10.2 (1, 118)

Table III-3. Distance-decay regression estimates for aquatic insects in varying categories of perceived threat. Bold font denotes slope estimates significantly different from zero (*=significant at p<0.1, **= significant at p<0.05, *** =significant at p<0.001).

	Ranking	Slope	r^2	F
All Parks	**G1 and G2**	**2.54E-04****	0.08	5.54 (1, 53)
	G3 and G4	**2.04E-04*****	0.11	15.79 (1, 118)
	G5	**9.78E-05***	0.01	3.18 (1, 134)
Parks (No GRSM)	**G1 and G2**	**2.64E-04****	0.1	5.63 (1, 43)
	G3 and G4	**2.01E-04*****	0.12	15.2 (1, 103)
	G5	8.92E-05	0.01	2.63 (1, 118)

Table III-4. Partial mantel tests on correlation between aquatic insect community dissimilarities and geographic/climatic distance correlations. Only Plecoptera community changes were significantly correlated with changes in climate/distance autocorrelation structure when all parks were considered. Removing GRSM improved the correlation and significance of the partial mantel test on all three insect order assemblages. *** denotes significance at p<0.05.**

	X	Y	Z	*r*	*p*
All parks	Geography	Environment	Ephemeroptera	0.284	0.08
	Geography	**Environment**	**Plecoptera**	**0.284**	**0.026***
	Geography	Environment	Trichoptera	0.2	0.059
No GRSM	**Geography**	**Environment**	**Ephemeroptera**	**0.372**	**0.006***
	Geography	**Environment**	**Plecoptera**	**0.47**	**0.001***
	Geography	**Environment**	**Trichoptera**	**0.359**	**0.005***

Table III-5a. Ephemeroptera. Null model probabilities that observed proportions of EPT species in any global imperilment ranks are larger than would be expected from a random draw from the regional species pool. P-values are one-sided; the lower the p-value the more likely that the observed frequency is larger than expected by random draws.

	G1	G2	G3	G4	G5
ABLI	1	1	1	1	0.509
BISO	1	0.773	0.81	0.865	0.174
BLRI	1	1	1	0.902	0.001
CHCH	1	1	1	0.947	0.053
COWP	1	1	1	1	0.213
CUGA	1	1	1	0.835	0.071
FODO	1	1	1	1	0.195
GRSM	0.834	0.996	0.92	0.885	0.005
GUCO	1	1	1	1	0.192
KIMO	1	1	1	1	0.044
LIRI	1	1	0.611	0.987	0.088
MACA	1	1	1	1	0.06
NISI	1	1	1	0.864	0.087
OBRI	1	1	1	1	0.037
RUCA	1	1	1	1	1
SHIL	1	1	1	0.923	0.109
STRI	1	1	1	1	0.193

Table III-5b. Plecoptera. Null model probabilities that observed proportions of EPT species in any global imperilment ranks are larger than would be expected from a random draw from the regional species pool. P-values are one-sided; the lower the p-value the more likely that the observed frequency is larger than expected by random draws.

	G1	G2	G3	G4	G5
ABLI	1	1	1	0.667	0.505
BISO	1	0.819	1	0.414	0.033
BLRI	1	0.772	0.705	0.039	0.587
CHCH	1	1	0.561	0.575	0.68
COWP	1	1	0.743	0.794	0.379
CUGA	1	1	0.829	0.743	0.049
FODO	1	1	1	1	1
GRSM	1	0.88	0.985	0.02	0.039
GUCO	1	1	1	1	0.069
KIMO	1	1	0.972	0.435	0.193
LIRI	0.829	0.754	0.974	0.009	0.853
MACA	1	1	0.702	0.956	0.132
NISI	1	1	0.615	0.673	0.658
OBRI	1	0.926	0.967	0.565	0.034
RUCA	1	1	1	0.381	0.709
SHIL	1	0.418	0.681	1	0.372
STRI	1	1	1	1	1

Table III-5c. Trichoptera. Null model probabilities that observed proportions of EPT species in any global imperilment ranks are larger than would be expected from a random draw from the regional species pool. P-values are one-sided; the lower the p-value the more likely that the observed frequency is larger than expected by random draws.

	G1	G2	G3	G4	G5
ABLI	1	1	0.863	0.94	0.048
BISO	1	0.993	0.994	0.999	0
BLRI	0.989	0.75	0.9	0.995	0
CHCH	0.879	0.995	1	0.964	0
COWP	1	1	0.962	0.992	0
CUGA	0.982	0.995	1	1	0
FODO	1	1	0.971	1	0
GRSM	0.999	0.987	0.924	0.592	0.001
GUCO	1	1	0.582	0.848	0.079
KIMO	1	1	1	0.928	0
LIRI	0.998	0.983	1	0.748	0
MACA	0.379	1	0.999	0.973	0
NISI	0.857	0.937	1	0.938	0
OBRI	0.992	0.995	0.996	0.976	0
RUCA	0.737	1	1	0.801	0.048
SHIL	0.938	1	1	0.674	0
STRI	1	1	1	1	0

Table III-6. Patterns of species richness in national parks. See Figure 1 caption for key to park abbreviations.

	Ephemeroptera	Plecoptera	Trichoptera
Total	129	136	359
ABLI	3	4	23
BISO	29	23	119
BLRI	48	57	213
CHCH	11	4	83
COWP	4	7	44
CUGA	15	16	94
FODO	5	0	28
GRSM	104	94	202
GUCO	4	4	22
KIMO	8	17	66
LIRI	17	26	108
MACA	12	11	92
NISI	15	5	59
OBRI	10	26	120
RUCA	0	3	13
SHIL	12	6	76
STRI	5	0	17

Table III-7. Patterns of occurrence of species in various categories of imperilment in national parks.

	G1	G2	G3	G4	G5
Total	18	41	63	102	400
ABLI	0	0	1	2	27
BISO	0	7	8	17	139
BLRI	3	18	30	46	221
CHCH	2	3	2	9	82
COWP	0	0	3	3	49
CUGA	1	3	4	9	108
FODO	0	0	1	0	32
GRSM	4	21	37	71	267
GUCO	0	0	2	2	26
KIMO	0	0	1	10	80
LIRI	5	6	4	20	116
MACA	2	0	3	7	103
NISI	1	2	1	8	67
OBRI	1	6	9	15	125
RUCA	1	0	0	2	13
SHIL	1	2	2	10	79
STRI	0	0	0	0	22

Table III-8. Patterns of species richness in state source pools.

	Ephemeroptera	Plecoptera	Trichoptera
Total	300	295	664
AL	138	89	366
AR	116	77	170
FL	76	29	156
GA	154	64	220
KY	135	110	290
LA	61	25	102
MS	58	47	141
NC	206	119	338
SC	182	77	308
TN	167	118	375
VA	168	160	352
WV	118	134	194

Table III-9. Patterns of occurrence of species in various categories of imperilment in state source pools.

	G1	G2	G3	G4	G5
Total	122	122	172	206	610
AL	40	39	58	84	372
AR	13	15	25	44	266
FL	20	23	22	33	163
GA	8	24	33	83	290
KY	6	17	41	76	395
LA	5	7	9	25	142
MS	5	12	19	25	185
NC	18	43	64	116	422
SC	13	31	55	95	373
TN	18	51	70	101	420
VA	12	25	72	106	465
WV	2	13	30	64	337

CHAPTER IV. CADDISFLY SPECIES TURNOVER ALONG HYDROLOGICAL GRADIENTS AND VARYING SOURCE POOLS

This chapter is a slightly modified version of a paper to be submitted for publication.

Robinson, J.L., C.R. Parker, D.A. Etnier and J.A. Fordyce. Caddisfly turnover along hydrological gradients and varying source pools.

ABSTRACT

Studies quantifying aquatic insect diversity among sites, habitats or areas may provide inferences on the functional responses of these groups to changes in available niches along ecological gradients, demographic processes structuring community assembly in stream networks or watersheds, or macroecological patterns of the coincident geographic ranges of species. However, when these studies are limited by imprecise taxonomic groupings, used when species-level identifications are difficult or impossible, estimates of the magnitude of the effects of these disparate processes may be confounded. Only *species* are united by common descent, demography and reproductive cohesion. Thus, there is no *a priori* theoretical expectation of the behavior of loosely defined aggregates of paraphyletic groups of species across spatial or environmental gradients. Previous researchers have used benthic data to compare patterns of variation among benthic macroinvertebrate assemblages, without considering the bias introduced by considering families or genera to be equivalent to *species*. Here, I analyze the effect of this taxonomic bias on tests of hypotheses on β diversity of assemblages of aquatic insets collected from different habitats in national parks in the southeastern highlands of the United States. These data are collections of spring and summer flying caddisflies (Insecta: Trichoptera), comprising 280 unique sampling events across five distinct habitat types (seeps, streams,

rivers, artificial reservoirs and unique wetlands). Species richness ranged from 2- 47 across samples. Across all parks, stream habitats had higher rates of per-capita species accumulation. Across all habitats, the Blue Ridge Parkway (BLRI) had a much higher species turnover and per-capita rate of species accumulation than other parks. Using species level identifications increased the value of estimates of β and γ diversity. Species turnover among headwater stream sites in Great Smoky Mountains National Park, (GRSM) was greater than among mid-order stream sites, but no significant differences were observed between these assemblages in these habitats along the BLRI. These differences were significant when considering both species and genera. Turnover along hydrologic gradients (i.e. within a watershed) is accomplished by turnover in both genera and species, reflecting ecological changes associated with stream size. Turnover along spatial gradients (i.e. along a transect crossing similar sites) may confound the effects of changes in source pool richness and changes in ecological factors associated with stream size and river continuum processes. Our results demonstrate using genus or family level data to measure turnover among sites can mask the sources of this variation. Even when specimens are identified to species, measures of turnover or dissimilarity across regions with varying source pools may fail to distinguish the proximal causes of variation among sites, since turnover in community composition among habitats can occur as a function of species replacement along transects or as a function of species sorting along environmental gradients.

Introduction

Processes generating beta diversity in headwater stream habitats have recently been the subjects of increased research attention among benthic ecologists (Clarke et al. 2008, Brown and Swan 2010, Finn and Poff 2011, Finn et al. 2011, Patrick and Swan 2011, Sokol et al. 2011). Mechanistically linking patterns of species richness to the generalized patterns of energy flow and availability predicted by the River Continuum Concept (RCC; Vannote et al. 1980) has remained a challenging problem, for reasons both conceptual and operational. Operationally, the data necessary to test macroinvertebrate community hypotheses are rarely sufficient to explore patterns of species distributions and instead treat genera or functional groups. Conceptually, it is unclear how the RCC could possibly be considered to predict patterns of species richness on the basis of abiotic parameters alone, and without considering species interactions or varying source pools.

For temperate forested watersheds, the RCC predicts patterns of variation in resource availability and the composition of environmental templates along a gradient of stream order or watershed size. In this view, biological communities are structured as a composite of functional responses to this gradient. For instance, small headwater streams have much higher surface area- perimeter ratios than larger streams with sunlit channels, with the result that leaf and woody debris inputs have a larger relative contribution to the trophic base of the benthic community in headwaters than primary production. As stream width increases, this ratio decreases and the relative contribution of primary production increases (Vannote et al. 1980). The composition of macroinvertebrate communities in these systems reflects these constraints: many experimental studies have demonstrated

higher abundance or diversity of wood and leaf shredder guilds in systems with higher allochthonous inputs (Wallace and Webster 1996).

These patterns of energy flow and resource dynamics are not in question, but considered alone do not intuitively predict anything about patterns of species richness in streams. Indeed, the word "richness" is not used in Vannote et al. (1980), which instead references the more vague term "diversity". The usage of "diversity" in ecology has been ambiguous; depending on the context the term can be interpreted to mean several different things (Tuomisto 2010, Anderson et al. 2011). Attempts to extend the RCC framework to explain patterns of species richness and/or diversity have included hypotheses about the effects of variation in the frequency of disturbance (Minshall et al. 1985a, Ward 1998, Burcher et al. 2007), tributary effects (Minshall et al. 1985b , Osborne and Wiley 1992), biotic "zones" (Rahel and Hubert 1991, geological history (Robinson and Rand 2005, Smith et al. 2010) and the geometry of species ranges (Dunn et al. 2006, Cucherousset et al. 2008). It is interesting to note that these extensions do not use the RCC to predict patterns of species richness or diversity but have instead drawn upon the RCC as an *ad hoc* potential explanation for observed patterns. Since the original RCC (Vannote et al. 1980) made no attempt to empirically or theoretically justify the claim that species richness should be highest in midsized streams or rivers, the persistence of this claim in the literature is curious.

Since the pool of potentially co-occurring EPT species can vary widely across similar habitats across broad regions (Vinson and Hawkins 2003, Boyero et al. 2012,

Chapter 3), it is not obvious that the RCC could possibly imply any particular pattern of species richness for aquatic insects (or even other taxa). Indeed, studies examining longitudinal patterns of species distribution or abundance along continuum gradients have not addressed the question of what should be the appropriate phylogenetic domain where community patterns might, in theory, be predicted by the RCC. In other words, considering only the response of a few selected taxonomic groups (such as fish, macroinvertebrates, diatoms, emergent plants, etc.) while ignoring all other groups of aquatic organisms provides at best an incomplete picture of the pattern purportedly predicted by the RCC, at worst misleading or inconsequential. Although Vannote et al. (1980, p. 135) briefly suggest that differing longitudinal patterns of "diversity" might be a contingent outcome of historical evolutionary processes among insects and mollusks or crustaceans (interactions between marine and freshwater adapted lineages), they apparently did not consider that the operation of such processes undermines the power of the RCC to explain patterns of species richness or diversity.

Other perspectives on the assembly of ecological communities, apart from the RCC, (e.g. Southwood 1977, Pringle et al. 1988, Death and Winterbourn 1995, Poff 1997, Fagan 2002, Leibold et al. 2004, Hubbel 2005, Muneepeerakul et al. 2008, Brown et al. 2011, Sokol et al. 2011) have emphasized the importance of network connectivity, dispersal, demographic processes, disturbance regimes and species interactions to contributing to differences in taxonomic composition among habitat patches, populations and communities. Any possible role for RCC-type processes in structuring aquatic insect communities (i.e., explaining the distribution of taxa as functional responses to resource

gradients) must also account for these ancillary phenomena. These processes describe the ecological or evolutionary behavior of individuals or populations of biological *species*: this necessarily requires a finer taxonomic resolution than is usually applied to benthic studies.

In this chapter, I present evidence that analyzing data on immature forms of aquatic insects is likely to mask patterns of species turnover, bias estimates of species richness and confound inferences on the mechanisms contributing to these patterns. Constraints on the identification of immature forms of aquatic insects may be imposed by morphological conservatism among immature forms of closely related species, or more generally by fundamental gaps in taxonomic knowledge (Cardoso et al. 2011). In some systems, the error contributed by low taxonomic resolution of specimen identifications may be negligible (Terlizzi et al. 2008). However, in freshwater stream systems, treating genera or families as operational taxonomic units is known to systematically bias indices of ecological integrity or biological water quality derived from benthic sampling data (Hawkins et al. 2000, Lenat and Resh 2001, Stribling et al. 2008, Houghton 2011, Sweeney et al. 2011, Yong and Hawkins 2011). As a simple example, genus level community data will always underestimate true species richness unless all species in samples are in monotypic genera. Richness estimators based on the abundance distribution of samples will also be compromised by this taxonomic error.

Although few studies have explicitly quantified the effect of this bias on the outcomes of hypothesis tests, in theory the effect could influence the results of many theoretical and applied aquatic ecology investigations. Research questions potentially

affected by these biases include the amount of taxa loss from degradation or land use (e.g., Stout and Wallace 2003, Pond 2010), measures of alpha or beta diversity across sites (e.g., Clarke et al. 2010, Finn et. al. 2011, Sokol et al. 2011, Sweeney et al. 2011), the prevalence of rare species in surveys (e.g., Resh et al. 2005, Siqueira et al. 2011), or the relative contribution of metacommunity processes to observed benthic assemblages (e.g., Brown and Swan 2010, Heino 2011, Patrick and Swan 2011).

For communities in the terminal tips of dendritic networks (like headwater streams), dispersal limitation among patches or habitats is likely to influence community composition, with the expected result that turnover among species might be higher among headwater stream reaches relative to mainstem communities (Fagan 2002, Meyer et al. 2007, Clarke et al. 2008, Finn et al. 2011). Yet, research on this question using immature life history stages of aquatic insects has failed to provide unequivocal evidence for the hypothesis that beta diversity is higher in headwater streams. Estimates of β diversity have been reported as both additive (Finn and Poff 2011) and multiplicative (Clarke et al. 2010) quantities estimated from abundance data, as well as in the form of community dissimilarities derived from presence-absence data (Finn et al. 2011, Patrick and Swan 2011). Other studies have found distance decay relationships in relative abundances or the prevalence of functional traits (Sokol et al. 2011); some have reported a lack of distance decay of compositional similarity in benthic macroinvertebrate assemblages (Finn and Poff 2011). These methodological differences preclude direct comparisons between these studies, and the aforementioned taxonomic limitations complicate the consideration of

alternative hypotheses (e.g, limits to dispersal or filtering along ecological gradients) where data on *species* are required.

Relative to turnover of species, turnover of genera among samples might reflect large shifts in resource availability or quality. Genera are often the fundamental taxonomic unit in published databases of the life history or ecological traits of benthic macroinvertebrates (e.g., Vieira et al. 2006), and much of the turnover in ecological traits may occur among genera (Bailey et al. 2001). Turnover in genera among sites is necessarily accompanied by turnover in species, but turnover in species not accompanied by turnover in genera could be the result of replacement from different source pools.

In this paper I test hypotheses on spatial patterns of species diversity, using data on species in the order Trichoptera collected during an inventory of aquatic insect species in national parks in the southern highlands of the United States. I quantify patterns of diversity among habitat types, among national parks and along environmental gradients, and then use these to test the hypothesis that turnover among species and genera is greater in headwater streams. I explicitly compare patterns of turnover between species and genera, in order to demonstrate how using taxonomically imprecise benthic data can confound patterns of turnover along ecological gradients with turnover associated with variation in gamma diversity.

Methods

We collected adult caddisflies from habitats in fifteen national parks across the southern and central Appalachians, Cumberland Plateau and Piedmont regions of the

southeastern United States (Fig. 1). All data reported here was collected with UV blacklight traps, placed near aquatic habitats and left overnight. Photovoltaic switches activate the lights at dusk, conserving enough energy that the lights usually remained on throughout the entire night until the traps were retrieved after dawn the next morning, thus applying a similar amount of collecting effort to each site. The contents of each trap were preserved, either by pinning or in ethanol, then sorted and identified to the lowest possible taxonomic level (species for males, species or genus for females) in the laboratory.

In addition to these collections, we used data from an additional park (Great Smoky Mountains National Park; GRSM) previously published in DeWalt and Heinhold (2005) and other unpublished collection events in the GRSM database (CR Parker, unpub. data). DeWalt and Heinhold (2005) used similar UV blacklight traps to sample adult aquatic insect assemblages in Cades Cove, a watershed consisting of Abrams Creek and several smaller order tributaries, during a span of several months. These GRSM collections sample along an extensive longitudinal gradient of stream order within the same watershed (and presumably the same source pool of species).

To remove seasonal variation in collections associated with changes in the efficiency of light traps during cool weather and unequal sampling effort applied to fall emerging taxa (i.e most species in families Limnephilidae and Neothremmatidae), I limit my analysis to samples collected during months April – August, encompassing the flight period for summer flying species of Trichoptera. To compare across broad categories of habitats, I initially grouped sites by habitat types immediately recognizable in the field (e.g. seeps and

springs, wadeable streams, large rivers, artificial reservoirs and natural wetlands). I estimated stream order from field observations (or from interpolation from computerized maps for large rivers) to improve the comparability among stream categories. For the purposes of these analyses, I distinguish between naturally occurring wetlands and reservoirs or artificially constructed ponds, but wetlands may vary by hydrology, water chemistry or vegetation characteristics across parks.

In order for explicit hypothesis tests to be comparable to previous studies, I grouped 1st (including springs and seeps) and 2nd order streams as "headwaters", and 3rd and 4th order streams as "mid-order" (following Finn et al. 2011). Bedrock geology and watershed geometry vary a great deal among (and even within) these parks, from strongly dendritic patterns in stream networks in the igneous-metamorphic Blue Ridge and Piedmont physiographic provinces to trellised and parallel drainage networks in the sedimentary formations of the Ridge and Valley and Cumberland Plateau. These natural variations are a confounder for comparisons by stream order or watershed area across different bedrock geologies; my use of stream order here is intended as a heuristic for categorizing streams with broadly similar channel dimensions and patterns of discharge, and does not imply a quantitative measure from field evaluations.

For visual comparison of the per-capita rate of species encounters, I constructed species accumulation curves among different parks and habitat types. To evaluate the effect of reduced taxonomic precision on these comparisons, I constructed a second dataset where taxa were identified only to genus. I used *R* package 'vegan' (2.0-3; Oksanen et al.

2012) to determine the exact species accumulation curve for each park and each habitat type (Uganda et al. 2003, Colwell et al. 2004).

In order to maximize the comparability to other studies, I tested the hypothesis that β diversity is greater in headwater streams using several different methods. To illustrate differences in diversity among parks or habitats, I calculated the multiplicative partition of α and β richness (q=0) and diversity (q=1) for both species and genera of Trichoptera (Jost 2006, 2007; R package 'vegetarian' (Charney and Record 2010)). I used bootstrapping to calculate the standard error of the partitioning into α and β. However, this does not provide a p-value for direct comparisons of between or among group diversity.

Multivariate dispersion tests the compare the variance around the distance to the centroid (of groupings of pairwise similarity measures) as another measure of beta diversity (Anderson et al. 2006). This method avoids issues of non-independence between pairwise comparisons. I used the R function *betadisper* to reduce the pairwise Jaccard and Sørensen dissimilarity matrices to principal coordinates, then used ANOVA and Tukey's Honest Signficant Difference test to compare dispersions among groups of habitat types (Oksanen et al. 2012).

Differences in regional source pools or position along environmental gradients might be expected to generate distance-decay in similarity of assemblages among sites. These effects should be evident at large spatial scales, associated with dispersal limitation, species sorting or changes in gamma richness (Astorga et al. 2012). We hypothesized that species turnover, in stream habitats, along the 700 kilometer transect of the BLRI would be

associated with changes in the source pool. To test this hypothesis, that proximal sites along the BLRI have more similar Trichoptera assemblages, I used the *raupcrick* function in *vegan* to compute pairwise dissimilarities for all stream samples (Oksanen et al. 2012). The Raup-Crick index is a dissimilarity measure that uses presence-absence data to estimate the probability that two samples are drawn from the same population (Chase et al. 2011). I then regressed these measures (both species and genera) onto geographic distances between BLRI sites, obtained from the mile markers, and tested whether the slope of these regressions were significantly different from zero.

Since changes along ecological and hydrological gradients occur within watersheds, turnover associated with these gradients should be evident in comparisons among habitats and at much smaller scales. At these small scales, turnover among genera of Trichoptera should be definitively associated with changes in ecological and resource gradients, and not differences in source pools. I calculated Jaccard and Sørensen dissimilarity indices and used t-tests to test the null hypothesis that there is no difference in the mean pairwise dissimilarity of headwater in mid-order streams in the GRSM and BLRI, for both species and genera datasets. Similarly, I tested the null hypothesis that there is no difference between species or generic richness between headwater and mid-order streams in GRSM and BLRI.

Results

I report here species occurrence data for 280 unique collection events, totaling 64,101 individuals belonging to 296 Trichoptera species in 63 genera. Species richness varied from 2 to 47 among collection events. Species accumulation rates varied among parks, but collections in BLRI had greater per-capita species and genera encounter rates than other parks (Fig. 2, 3). Stream habitats were most heavily sampled across all parks, with 156 collections in streams, more than three times as many sites as the next most frequently sampled habitat type (Table 1). Stream habitats accumulated taxa (both species and genera) at a greater per-capita rate than all other habitat types, even compared at small sample sizes (Fig. 4, 5). Non-stream habitat types accumulated species at similar rates.

Multiplicative partitioning of diversity among habitats

Across all samples, for abundances (q=1), the multiplicative partition of β diversity is more than twice the value of α (Table 2). When samples are identified to lower precision (i.e., genus level taxonomy was used instead of species), β is more similar to α (γ diversity decreased nearly fourfold). Among habitat types, the greatest values of β diversity were observed among stream habitats, for both species and genera datasets. Values of β are similar among habitat types in both the genus and species datasets.

Considering patterns of presence-absence only (q=0) changes the partitioning of diversity among habitats and in the total dataset (Table 3). When q=0, β is higher than α for streams and seeps and across all habitats overall. However, values of α are higher than

β for rivers and bogs, and approximately equal for pond habitats. When considering only genera, β is lower than α among all samples and habitats.

Multiplicative partitioning of diversity among parks

Among all parks, when q=1, β is more than twice the value of α for species but only slightly larger for genera (Table 4). Only 3 parks had greater values of β than α for species diversity (BLRI, GRSM and MACA). For genera, measures of β within parks were always lower than α, with the exception of GRSM. Considering genera alone, when q=1, reduced γ (across all parks) by a factor of more than 3 (Table 5). When q=0, for both species and genera, no individual park had greater values of β than α.

Multivariate dispersion tests

Across all habitat types, for multivariate dispersion tests built from presence-absence data, headwater assemblages had significantly greater distances to the group centroid than did headwater streams, for both species (Figure 6) and genera (Figure 7). In other words, Trichoptera assemblages from headwater stream sites were significantly more dissimilar than collections from mid-order stream sites, even when considered at the coarser taxonomic grain associated with greater ecological differences among taxa. Additionally, headwater stream assemblages were more dissimilar than river habitats, for both species and genera. Comparisons among pond, river and bog assemblages do not reflect assemblages within every park, since some parks did not have some habitat types (Table 1).

Distance decay of similarity along BLRI

We detected a weak distance-decay of similarity among BLRI streams, for BLRI streams (Fig 8), demonstrating spatial structure of Trichoptera species assemblages that might be associated with changes in the source pool of species. We detected no statistically significant distance decay of similarity among BLRI streams among genera (Fig 9).

Comparing headwater and mid-order assemblage dissimilarity along spatial and environmental gradients

We found no difference in the mean dissimilarity of adult Trichoptera assemblages collected from headwaters and mid-order streams along the BLRI, for neither species nor genera. This was true whether dissimilarities were calculated from abundances or incidences. However, in both cases, GRSM headwaters had significantly greater mean dissimilarities than mid-order streams, and this pattern held for both incidence (Fig. 10) and abundance based dissimilarities (Fig. 11, Table 6). In other words, in GRSM there is greater turnover among genera and species in headwater streams than in mid-order streams. This is in strong contrast to BLRI streams, where community dissimilarity measures among headwaters and mid-order streams were not different for either metric or taxonomy.

Headwater streams in GRSM have lower species (t= -5.89, df= 30.6, p<0.0001) and generic (t= -6.45, df=38.16, p<0.0001) richness than do GRSM mid-order streams (Figure 12). I found no significant difference in species or generic richness, between headwater and mid-order streams along the BLRI. BLRI headwater streams did not have significantly

higher species richness than GRSM headwater streams, but did have higher generic richness (t= -3.53, df=65.77, p <0.001). GRSM and BLRI mid-order streams did not have significantly different richness of species or genera.

Discussion

The generalization that species richness of aquatic insects tends to be low in headwater streams, relative to larger downstream segments, has been broadly supported by both empirical studies and theoretical representations of metacommunity dynamics (Meyer et al. 2007, Clarke et al. 2008, Finn and Poff 2011, Finn et al. 2011, Patrick and Swan 2011). What has received less support, or has been less adequately tested, is the hypothesis that turnover among species is greater in headwater habitats, relative to larger downstream segments. The *a priori* theoretical expectation for such a pattern is clear: colonization and extinction dynamics might produce this pattern simply as a consequence of small population sizes and dispersal limitation in isolated headwater reaches of dendritic networks (Fagan 2002). However, prior attempts to test this hypothesis have confounded turnover in source pools with turnover along the river continuum from headwaters to mid-order reaches. Imprecise taxonomic categories facilitate this error; turnover in genera is always accompanied by turnover in species but turnover of species within genera might not be recognized from identifications of immature aquatic insects. In this chapter I have used data on adult caddisfly species occurrences, eliminating the uncertainty around the actual values of species richness and diversity, to demonstrate different sources of species turnover in this dataset.

In Chapter 3 of this dissertation I presented evidence that the aquatic insect assemblages in national parks in this study are drawn from different source pools. This is a constraint on direct comparisons of species diversity among sites across parks, but some generalizations are possible. Collections made in stream habitats accumulate species at a greater per-capita rate than collections made from other habitats, and the partitioning of diversity (among sites) varies a great deal among parks and habitats. Only BLRI has all types of habitats represented in this dataset. In all instances, considering only occurrences of genera, analogous to the results from benthic studies, underestimates species richness and turnover among units. Understanding the processes that have contributed to the formation of disparate source pools across this region is a key goal of macroecology is a key to understanding spatial patterns of species occurrences within watersheds.

The Blue Ridge Parkway (BLRI), in NC/VA, is notable as an exception to the general pattern of per-capita species accumulation exhibited by these parks. As a 700 km long transect across the headwaters of many major stream systems, the BLRI is the only park in this study that is large enough to traverse the complete range of individual species. Several aquatic salamander species in the genus *Desmognathus* (Plethodontidae) are restricted to small portions of the Blue Ridge mountains, which are likely a dispersal barrier between species that occur more widely (Tilley and Mahoney 1996, Tilley et al. 2008). Among caddisflies, several species are known only from areas at one end of the parkway or the other (i.e *Adicrophleps hitchcocki* Flint (Brachycentridae), *Rhyacophila accola* Flint (Rhyacophilidae), *Homoplectra monticola* Weaver (Hydropsychidae) and others). A linear transect across this region should result in the BLRI sampling a larger source pool of

Trichoptera species than a single large park in a single area (e.g. GRSM). That many other aquatic species share similar patterns of distribution, with less vagile dispersal stages than winged aquatic insects, suggests that dispersal limitation might be partly responsible for the structure of caddisfly assemblages along the BLRI.

Directly demonstrating that dispersal limitation is a force which structures aquatic insect communities is impossible without empirical measurements of species-specific dispersal behavior in sites with varying degrees of network connectivity. However, the result that the pairwise similarity of stream caddisfly assemblages decays with distance (along the BLRI) is consistent with dispersal limitation among sites. Alternatively, it might be that gradients in some aspect of stream habitats or other niche parameters are responsible for the separation of some species to one end of the BLRI or another (distance decay of environmental similarity). However, since genera of aquatic insects often have distinct syndromes of ecological traits (Poff et al. 2006), the lack of distance decay of similarity among caddisfly genera suggests that species turnover (along the BLRI) might occur by replacement of ecologically analogous species within genera.

Linear transects across headwater streams, like the BLRI, offer an opportunity to measure turnover among sites organized along spatial gradients, emphasizing variation in source pools. Alternatively, in GRSM it is possible to observe caddisfly assemblages along the hydrological continuum from headwaters to larger stream segments. River continuum theory predicts changes in resource availability (e.g., particulate organic matter, primary production) as a function of watershed position and stream order. Accordingly, the

distributions of aquatic insect taxa along these gradients are some of the best known examples of functional responses (to trophic structure) known in ecology (Cummins 1973).

I have assumed that sites within a watershed share a source pool of potential colonizing species. While there are species of Trichoptera known only from a single or a few sites in GRSM (e.g., *Homoplectra flinti* Weaver*, Lepidostoma sackeni* (Banks)*, Rhyacophila Montana* Ross*, Neophylax kolodskii* Parker; CR Parker unpublished data), those species did not occur in this dataset and those sites were not sampled. Whether those species are in fact limited to those sites within GRSM is unknown, but to the extent that the assumption of a shared source pool holds (for this dataset), then the turnover in species occurrences among these sites in GRSM is some function of species-sorting and colonization-extinction dynamics among habitat patches. In particular, the contribution of species sorting along the river continuum is most relevant to understanding how the bias imposed by imprecise identifications might affect measures of diversity, since species replacement within genera will not be detected by taxonomic methods which do not differentiate between species.

Previous researchers have found evidence for the hypothesis that headwater streams have lower alpha diversity and greater beta diversity than mid-order streams (Finn and Poff 2011, Finn et al. 2011). One study, examining turnover among benthic macroinvertebrate taxa in several small watersheds in Australia, sampled along a continuum of stream size similar to this study (Clarke et al. 2010). Interestingly, that study found low turnover among benthic assemblages in headwater streams and suggested that

30 m reaches contained a high proportion of the total macroinvertebrate diversity in the study area, but failed to identify specimens to species. The results I present here demonstrate how such a pattern might be observed yet be an artifact of taxonomic imprecision: along the BLRI I found no difference in the average dissimilarity of headwaters or mid-order streams (among species or genera), but I did observe a decay of the similarity of species assemblages with distance that was not replicated among genera.

That larger stream segments in GRSM have more Trichoptera species and genera than headwaters is not a surprising result. Mid-order stream habitats are often adjacent to or contain habitats similar to confluent tributary streams (e.g., tributary effects (Minshall et al. 1985, Osborne and Wiley 1992)), which could influence local species richness. It is tempting to simply ascribe these differences in species richness to the "prediction" made by the RCC that "diversity should increase in mid-order reaches" as a function of habitat and trophic diversity (Vannote et al. 1980). I find that unsatisfactory for several reasons, but perhaps the simplest objection is to consider that these streams are among the headwaters of the Tennessee River, which ultimately flows into several larger rivers and the Gulf of Mexico. In that context, it seems unreasonable to consider Abrams Creek a "mid-order" reach of the entire stream system.

Semantics aside, it remains likely that mid-order species richness is higher, in these samples, as an outcome of river continuum processes structuring the distribution and abundance of available niches within the stream. If that is true, then the failure of Trichoptera species and genera in BLRI streams to generate the same pattern might be a

function of varying source pools among the pairwise comparisons. Although I have not attempted to identify or account for dispersal barriers, this remains a potential mechanism for shaping regional diversity patterns along the Blue Ridge.

Aquatic insect dispersal remains a tedious and difficult process to study: the direction and magnitude of dispersal patterns can vary with the ontogeny of individuals, among populations, species within genera or even higher levels of organization or across land uses and riparian zone quality (Hughes et al. 1998, Griffith et al. 1998, Petersen et al. 1999, Smith et al. 2009, Malison et al. 2010). Efforts to detect even low levels of dispersal may require intense and highly structured sampling of large numbers of individual insects, which in turn requires a great deal of effort by taxonomic specialists to identify and database. This knowledge gap poses problems to biological monitoring of water quality and ecological restoration objectives which preferably weight higher species richness and abundances, predicated upon the assumption that species abundances are locally determined by environmental characteristics and not dispersal limitation. Thus, understanding how the ecology of adult life history stages influences patterns of abundance and diversity of immature forms systems remains a collective goal of ecologists and resource managers alike.

Thus, I cannot distinguish between hypotheses on the geometries of the geographic range of species, and hypotheses that species turnover among caddisfly assemblages in headwater streams is a function of dispersal limitation between sites. However, at first reckoning, dispersal based explanations seem unpalatable to my biological intuition.

Anecdotes of long distance dispersal of winged insects abound. During the course of this study I collected adult Hydropsychid species typical of larger riverine systems from ponds, swamps, and even in my backyard approximately one mile from the Tennessee River. Massive dispersal events of some large river species are common entomological lore: mass emergences of species in the mayfly genus *Hexagenia* (Ephemeroptera: Ephemeridae) have been detected via radar (Masteller and Obert 2000). Winterbourn et al. (2007) document a broad range of dispersal behaviors, including overland flight. Similarly, MacNeale et al. (2005) documented interbasin transfers and riparian dispersal of *Leuctra* sp. of stoneflies (Plecoptera: Leuctridae) in a small watershed at Hubbard Brook (NH, USA).

However, these dispersal behaviors might reflect general ethological disparities in dispersal propensity between species adapted for lentic habitats (or large river species) and species restricted to headwater streams. The potential success of a successful long-distance dispersal event is in part a function of the number of propagules, which is in turn a function of population size (Wright 1951). Even if density remains constant, population size for large river species will be greater, per unit stream length, than in smaller streams. We did not systematically sample benthic habitats in this study, but comparing benthic and aerial assemblages of aquatic insects collected from the same habitats might elucidate factors contributing to establishment success among species (and therefore demography or life history traits).

Although we cannot determine the location of the emergence of individuals from collection records, it seems obvious that (for some species, at least) caddisflies may disperse into marginal or sub-optimal habitats during the duration of the winged adult stage. Further, since population sizes of species inhabiting these vast riverine habitats must be orders of magnitude larger than population sizes of seep and headwater stream specialists, these systems provide an ideal scenario for studying the relative importance of mass effects, and species sorting, to metacommunity dynamics. Variation in patterns of adult dispersal, manifesting in individuals, populations or species, has the potential to strongly affect the ecology and evolution of stream insects in many distinct ways already predicted by theory (Sokol et al. 2011). These patterns are likely to emerge only with the careful application of coordinated adult and immature sampling strategies that can collect data to adequately test distinct community assembly hypotheses.

Species diversity in headwater streams is a function of processes acting at multiple spatial scales. Quantifying these patterns requires data with the appropriate taxonomic precision and an adequate spatial coverage for testing alternate hypotheses. Attempts to measure turnover among higher taxa, or at large spatial scales will likely confound the effects of ecological gradients and spatial gradients (source pools). Further refinement of metacommunity analyses in aquatic insect ecology should focus on patterns of dispersal and colonization, which necessarily require the coordinated sampling of both adult and larval life history stages across seasons. Finally, robust estimates of the geographic range occupied by species of aquatic insects will greatly enhance estimates of regional source pools and refine analyses of diversity along gradients.

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APPENDIX IV. Figures and Tables.

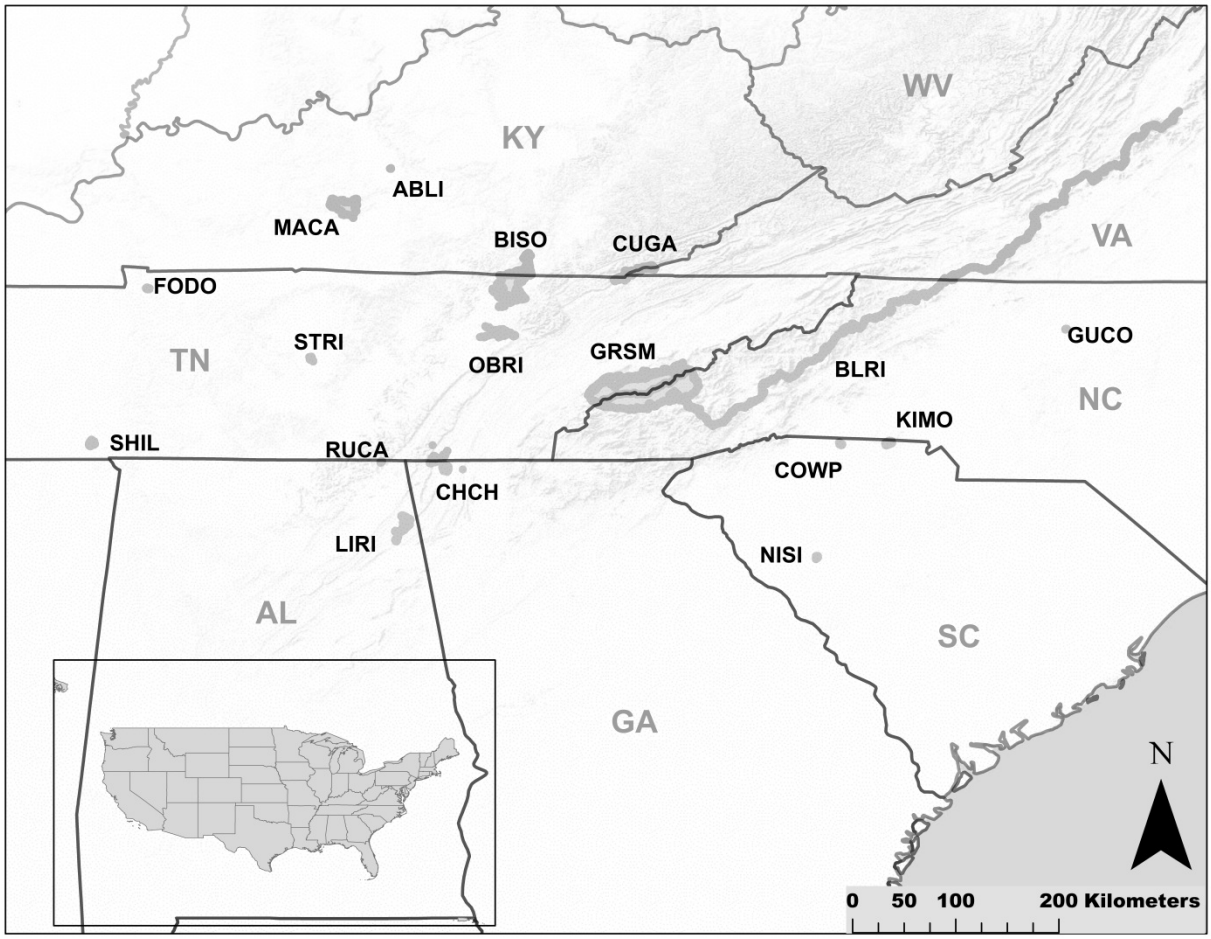

Figure IV-1. Map of southeastern United States and parks sampled in this study. Abbreviations are as follows: ABLI- Abraham Lincoln Birthplace National Historical Park, Hodgenville, KY; BISO- Big South Fork National River and Recreational Area, Oneida, TN; BLRI- Blue Ridge Parkway, Asheville, NC; CHCH- Chickamauga and Chattanooga National Military Park, Fort Oglethorpe, GA; CUGA- Cumberland Gap National Historical Park, Middlesboro, KY; COWP- Cowpens National Battlefield, Chesnee, SC; FODO- Fort Donelson National Battlefield, Dover, TN; GRSM- Great Smoky Mountains National Park, Gatlinburg, TN; GUCO- Guilford Courthouse National Military Park, Greensboro, NC; KIMO- Kings Mountain National Military Park, Blacksburg, SC; LIRI- Little River Canyon National Preserve, Fort Payne, AL; MACA- Mammoth Cave National Park, Mammoth Cave, KY; NISI- Ninety Six National Historic Site, Greenwood, SC; Obed Wild and Scenic River, Wartburg, TN; RUCA- Russell Cave National Monument, Bridgeport, AL; SHIL- Shiloh National Military Park, Shiloh, TN; STRI- Stones River National Battlefield, Murfreesboro, TN.

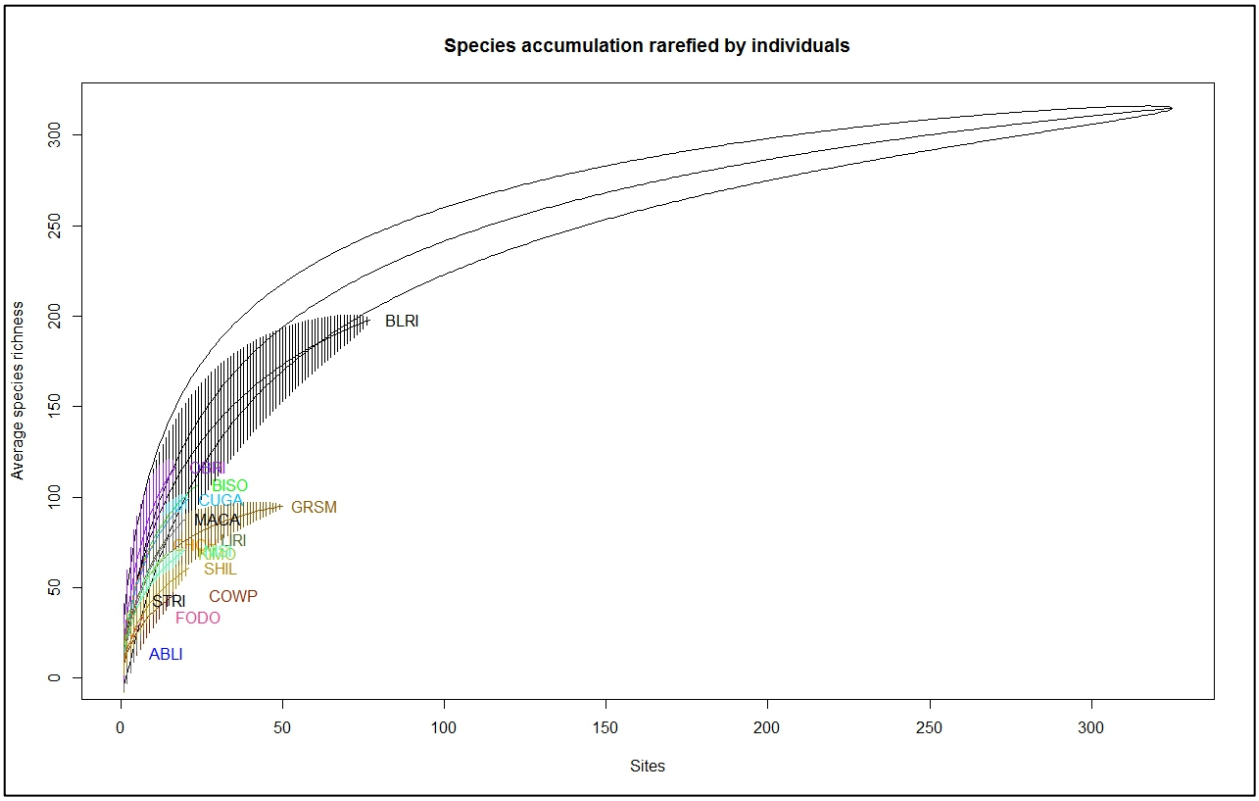

Figure IV-2. Species accumulation curves per site, rarefied by individuals, for 16 national parks. Hollow shaded curve is the species accumulation curve for all samples. Shaded area is 95% confidence interval calculated from resampling. BLRI has more sites but also accumulates species at faster rate than other parks with larger numbers of sites.

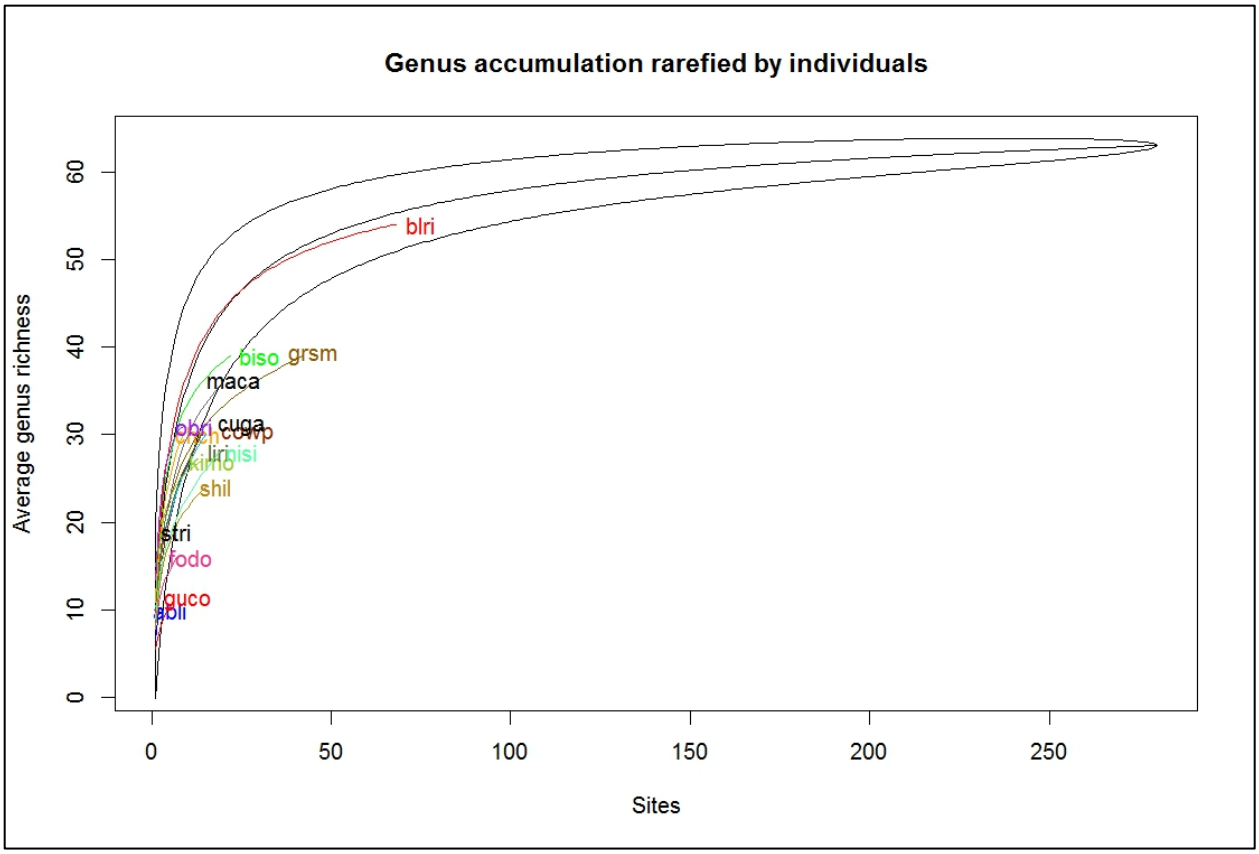

Figure IV-3. Genus accumulation curves per site, rarefied by individuals, for 16 national parks. Hollow shaded curve is the species accumulation curve for all samples. Confidence intervals are removed for ease of visualization of pattern. BLRI accumulates genera at greater rate than all other parks, at similar sample sizes.

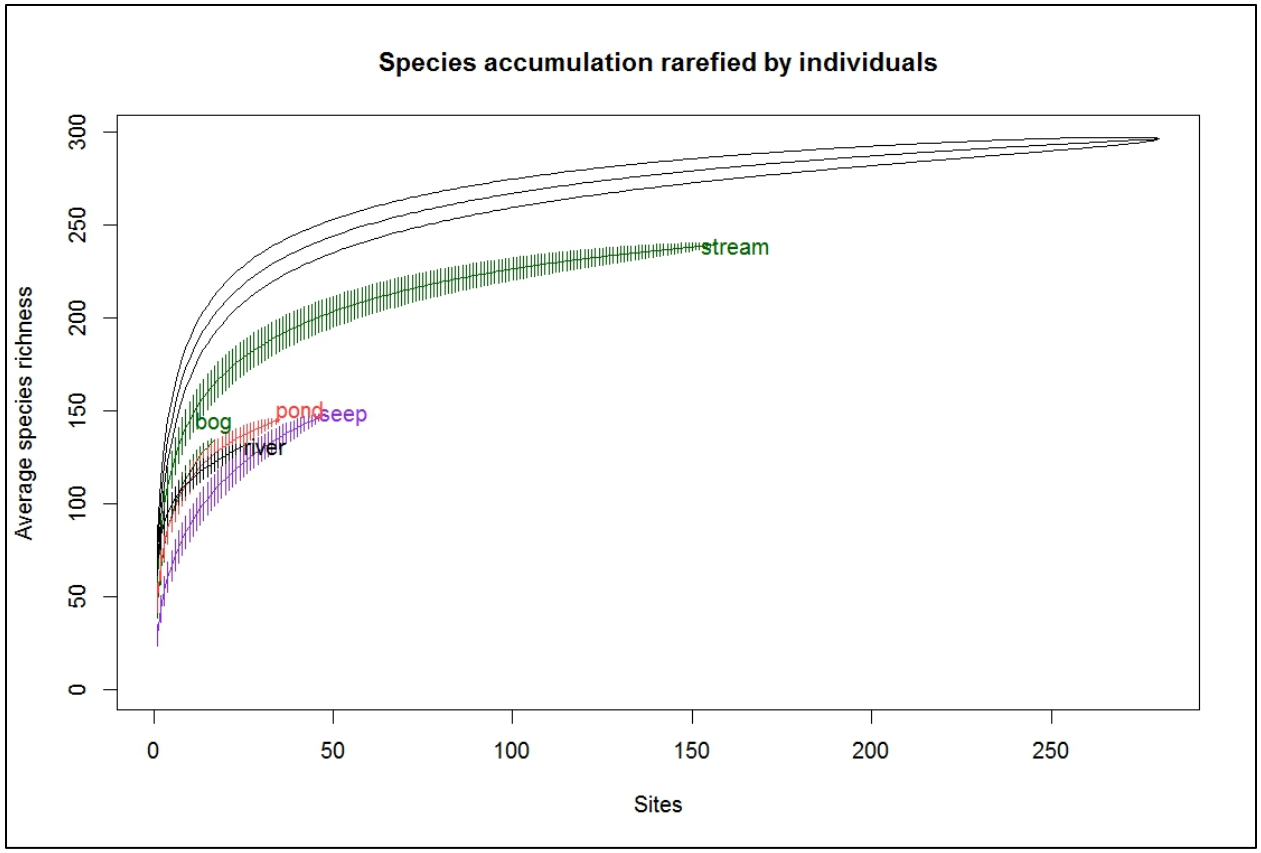

Figure IV-4. Genus accumulation curves per site, rarefied by individuals, for 16 national parks. Hollow shaded curve is the species accumulation curve for all samples. Confidence intervals are removed for ease of visualization of pattern. BLRI accumulates genera at greater rate than all other parks, at similar sample sizes.

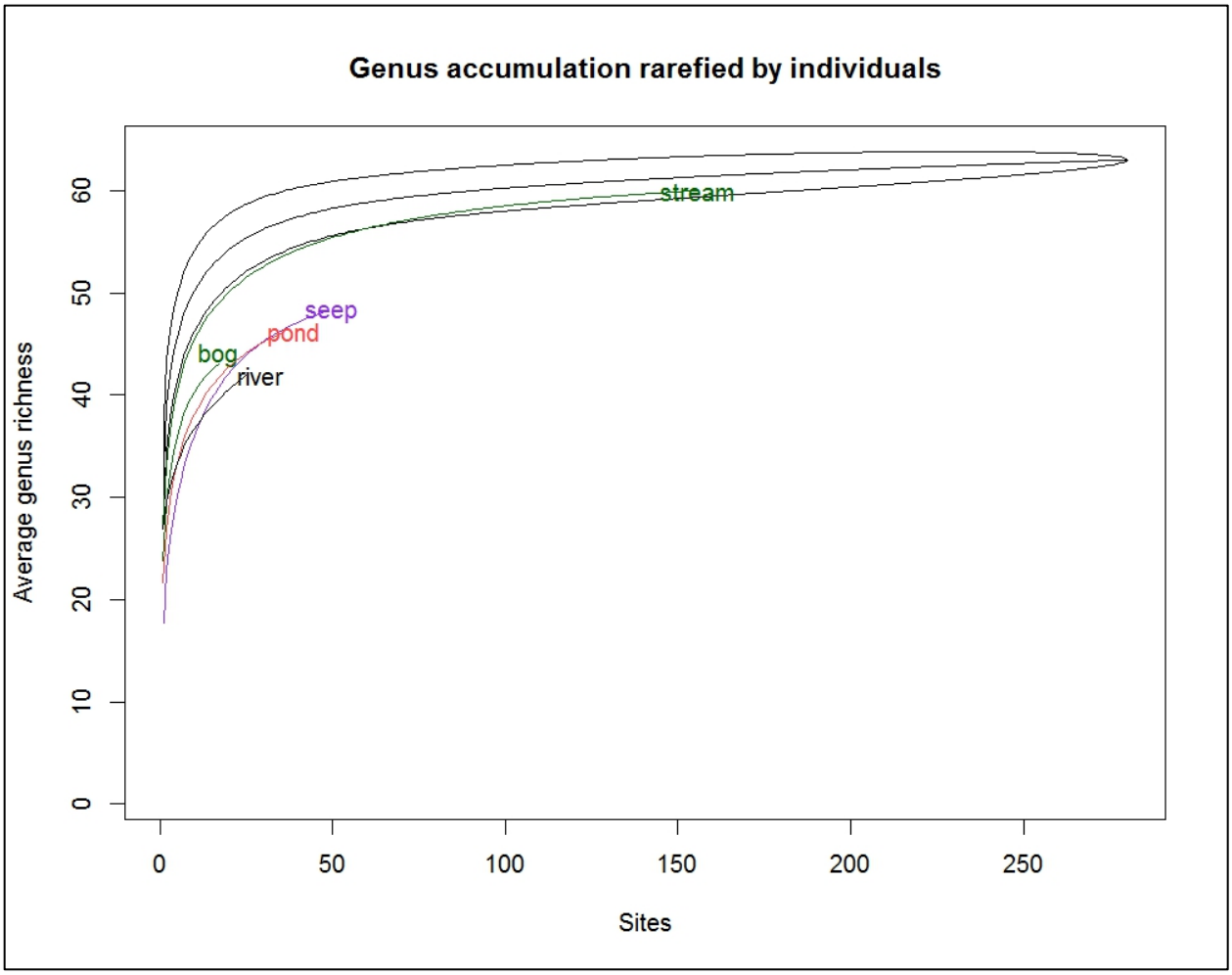

Figure IV-5. Genus accumulation curves in different habitats, rarefied by individuals, across 16 national parks. Hollow shaded curve is the species accumulation curve for all samples, confidence intervals around habitat curves removed for ease of visualization of patterns. Stream habitats accumulate genera at greater rate than all other habitats, even at low sample sizes.

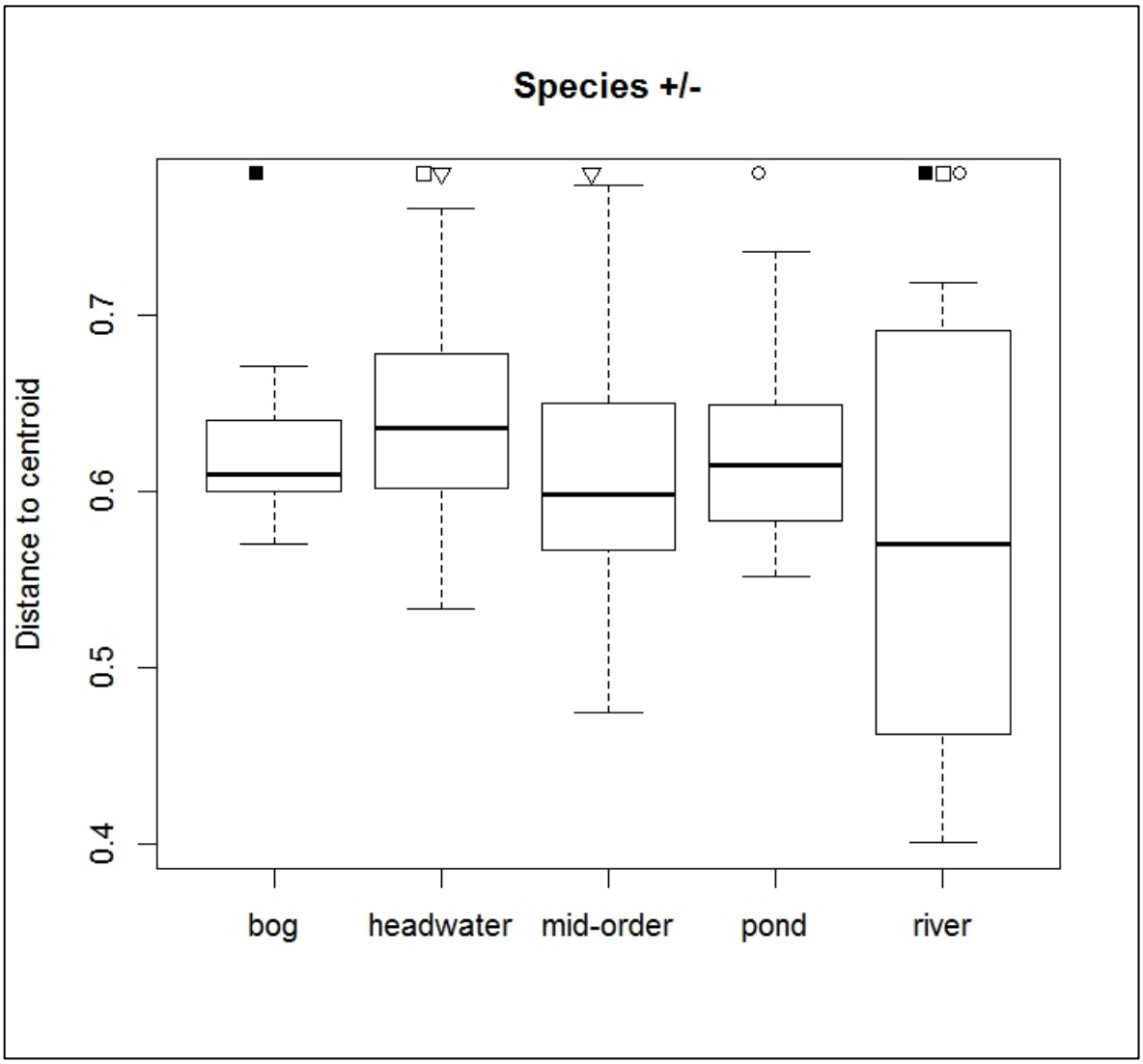

Fig. IV-6 Multivariate dispersion of Jaccard community dissimilarities among sites in each habitat type. Symbols at top of graph denote pairwise significant differences (Tukey HSD). Solid symbols denote $p<0.05$, hollow symbols denote $p<0.01$.

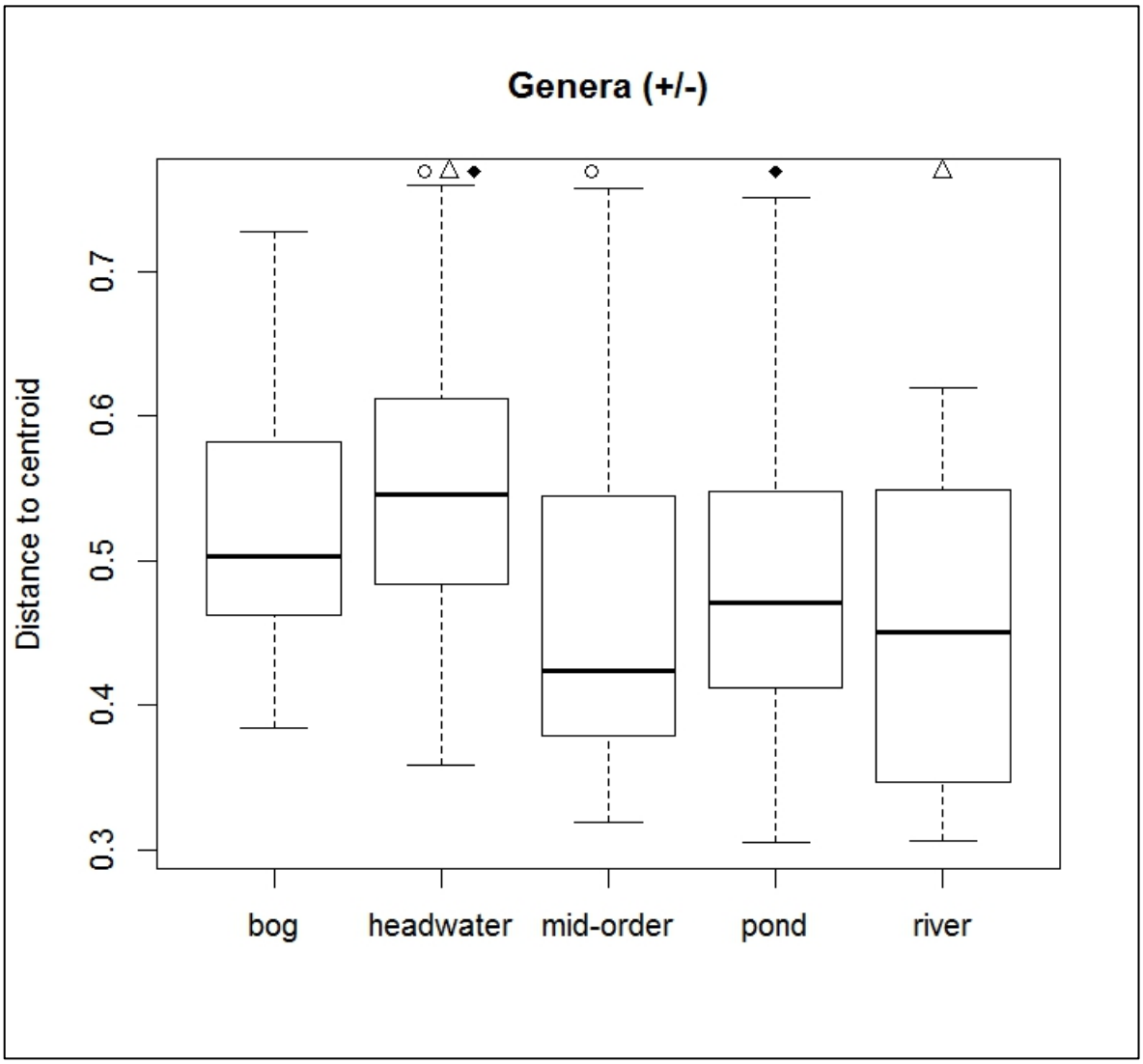

Figure IV-7. Multivariate dispersion of Jaccard community dissimilarities among sites in each habitat type. Symbols at top of graph denote pairwise significant differences (Tukey HSD). Solid symbols denote $p<0.05$, hollow symbols denote $p<0.01$.

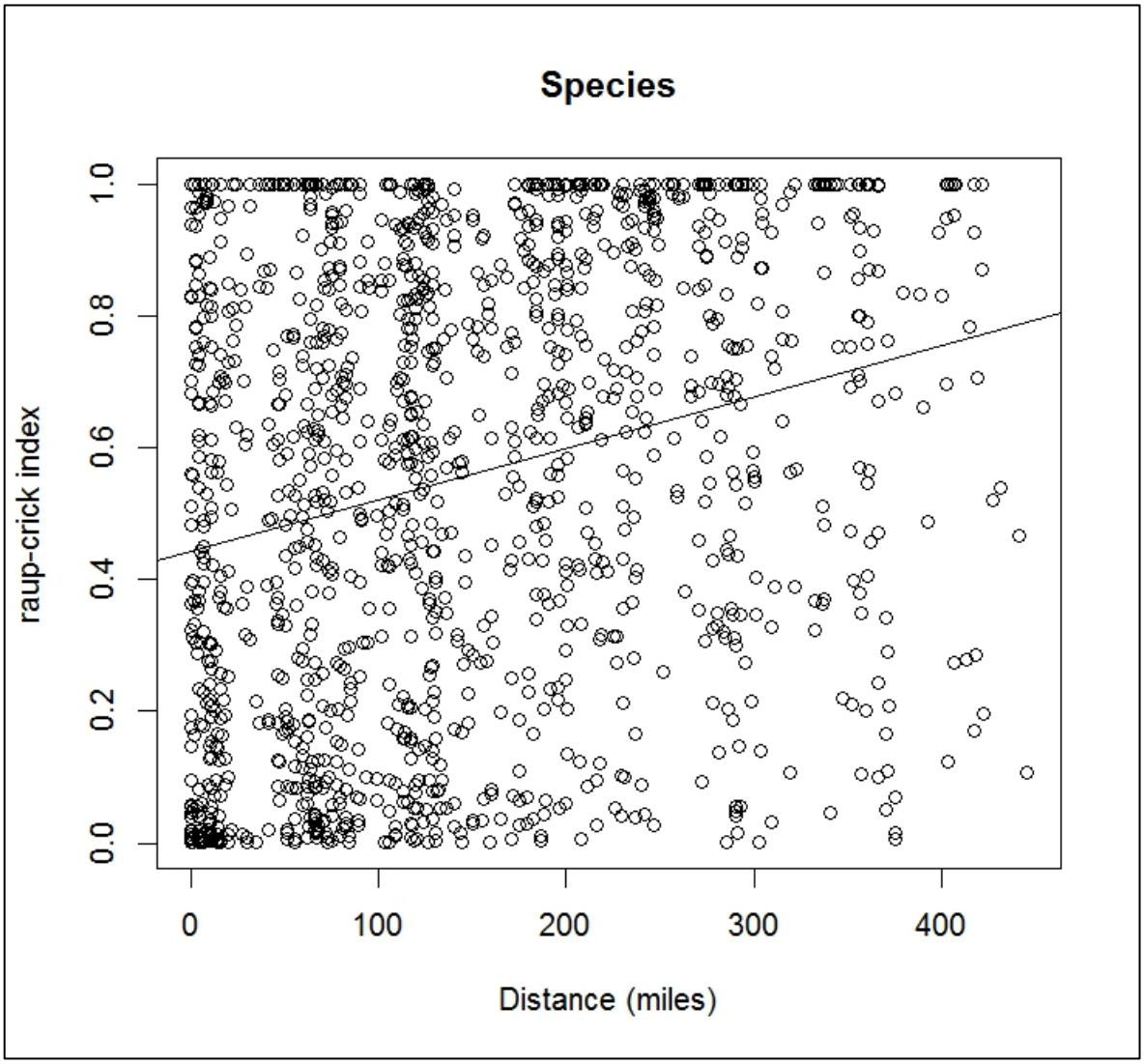

Figure IV-8 Distance decay of Raup-Crick similarity among Trichoptera species assemblages in streams on the Blue Ridge Parkway (BLRI). The slope of the regression line is significantly different from zero (slope= 0.0008, $p<.001$, $F_{1, 1376} = 89.9$, $r^2 = 0.06$).

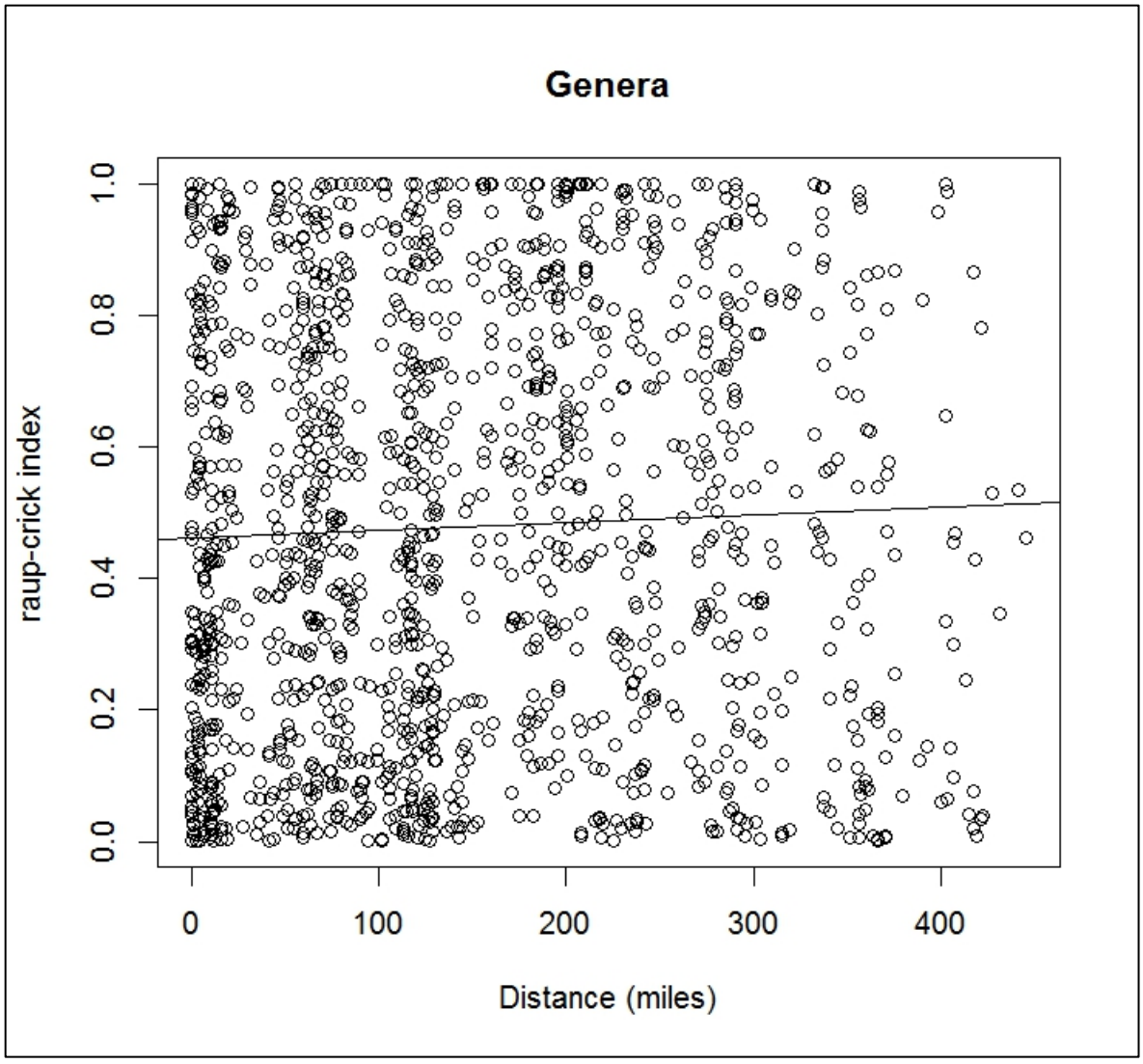

Figure IV-9. Distance decay of Raup-Crick similarity among Trichoptera genera assemblages in streams on the Blue Ridge Parkway (BLRI). The slope of the regression line is not different from zero ($p=0.16$, $F_{1, 1376}= 2.0$, $r^2=0.0007$).

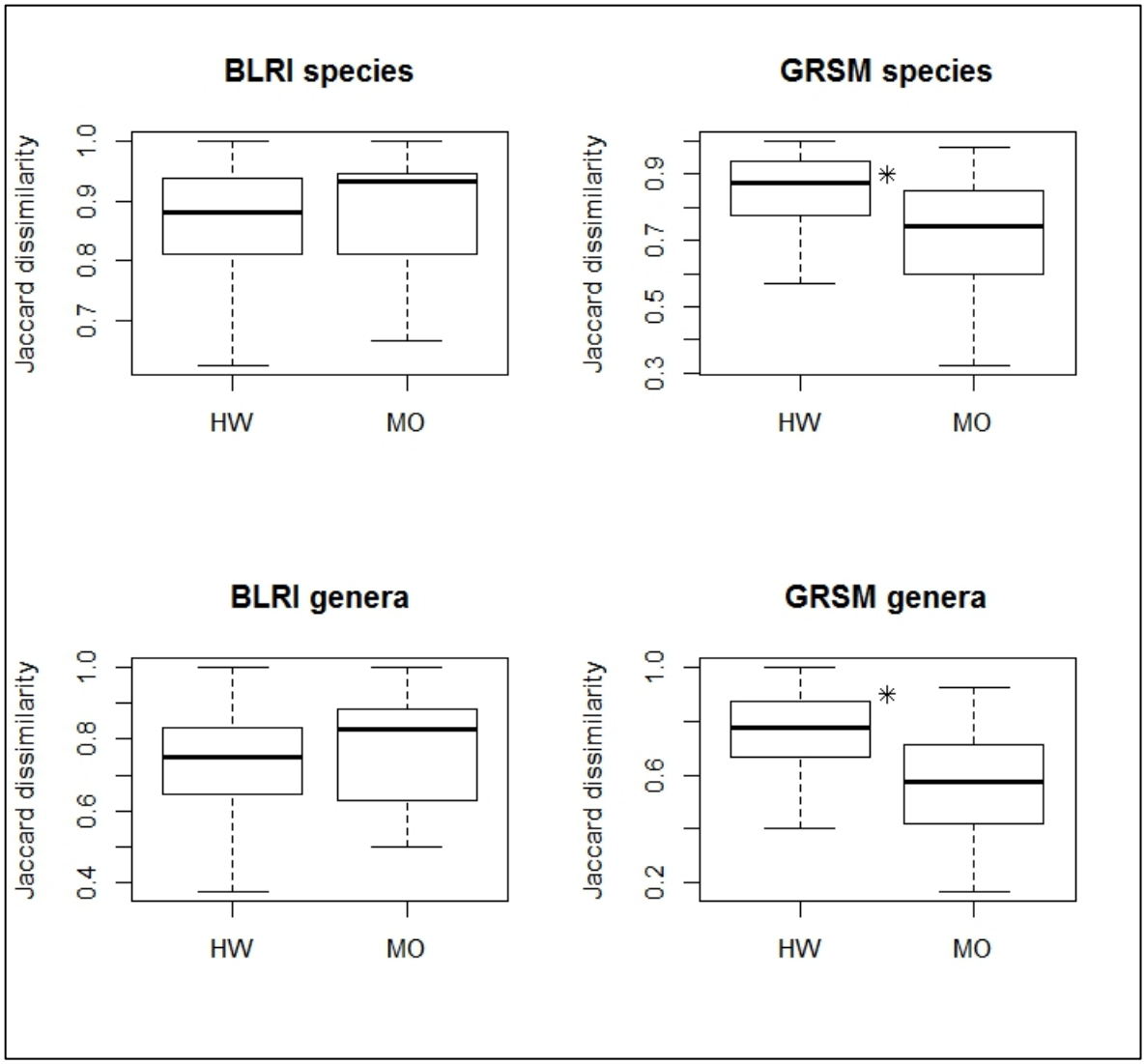

Figure IV-10. Jaccard dissimilarity of Trichoptera assemblages in headwater (HW) and mid-order (MO) streams in Blue Ridge Parkway (BLRI) and Great Smoky Mountains (GRSM) national parks. * denotes significant difference at $p<0.0001$.

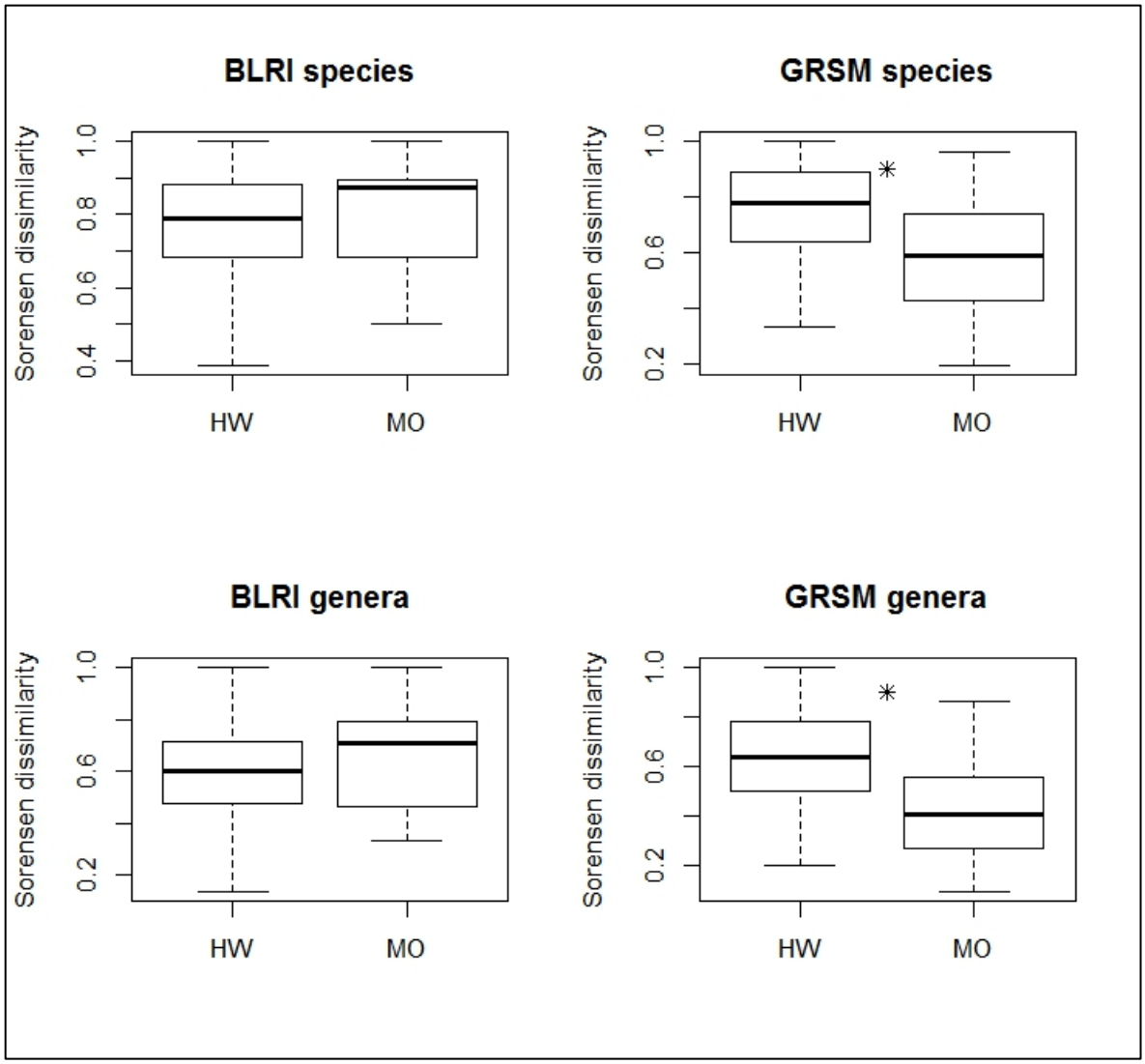

Figure IV-11. Sorensen dissimilarity of Trichoptera assemblages in headwater (HW) and mid-order (MO) streams in Blue Ridge Parkway (BLRI) and Great Smoky Mountains (GRSM) national parks. * denotes significant difference at $p<0.0001$.

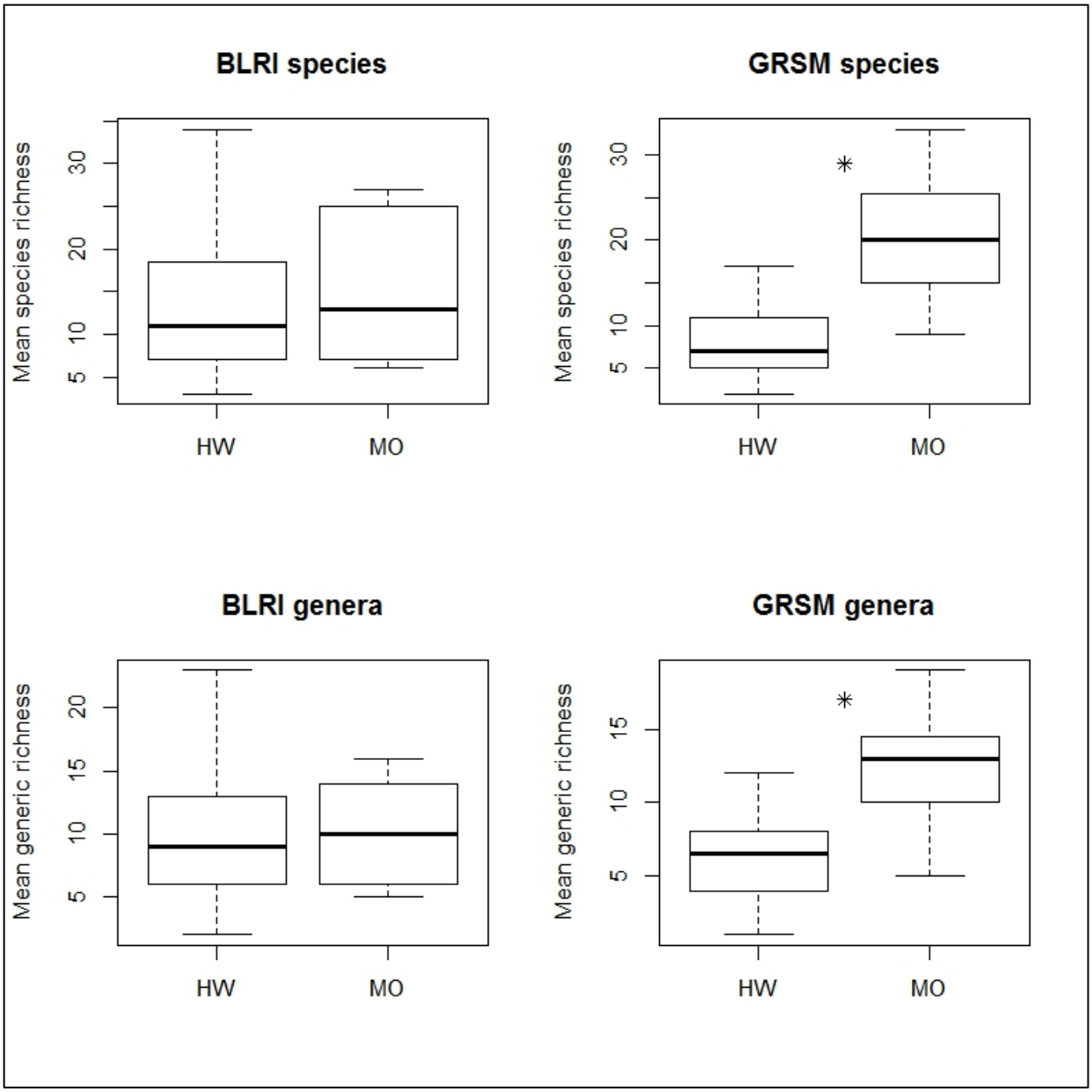

Figure IV-12. Headwater streams in GRSM have lower species and generic richness than mid-order streams. There is no difference in richness among BLRI headwater and mid-order streams for either taxa.

Table IV-1. Total number of collections taken from each of five habitat types in each park during the course of this sudy.

Park	Wetland	Pond	Headwater	Mid-Order	River	Total
ABLI	0	1	0	1	0	**2**
BISO	0	6	3	3	10	**22**
BLRI	7	7	48	5	1	**68**
CHCH	1	0	6	2	0	**9**
COWP	0	0	14	0	0	**14**
CUGA	3	0	10	2	0	**15**
FODO	0	0	5	0	2	**7**
GRSM	0	0	22	20	0	**42**
GUCO	0	0	4	2	0	**6**
KIMO	0	0	9	5	0	**14**
LIRI	2	0	12	0	0	**14**
MACA	2	5	11	0	2	**20**
NISI	0	11	0	8	0	**19**
OBRI	0	0	2	6	1	**9**
SHIL	2	3	9	0	1	**15**
STRI	0	2	0	2	0	**4**
Grand Total	**17**	**35**	**155**	**56**	**17**	**280**

Table IV-2. Multiplicative partition of species and generic diversity among five aquatic habitat types, based on resampling (n=100) of abundance matrix. Standard errors given in parentheses.

Abundance Matrix (q=1)

species	α	β	γ	genera	α	β	γ
total	6.13 (0.05)	14.83 (0.2)	90.92(1.20)	total	4.63 (0.03)	5.04 (0.05)	23.38 (0.23)
stream	6.53 (0.06)	11.39 (0.19)	74.42 (1.02)	stream	4.95 (0.05)	4.36 (0.06)	21.58 (0.28)
bog	6.73 (0.2)	7.12(0.18)	47.89(1.34)	bog	5.07 (0.14)	3.23 (0.09)	16.39 (0.58)
river	6.48 (0.11)	6.97 0.15)	45.14(1.14)	river	4.93 (0.09)	3.28(0.08)	16.19 (0.43)
seep	5.66 (0.11)	7.58(0.29)	42.91(1.34)	seep	4.67 (0.10)	3.82 (0.11)	17.84 (0.44)
pond	4.72 (0.1)	6.64(0.18)	31.35(0.96)	pond	3.14 (0.06)	2.93 (0.07)	9.23 (0.21)

Table IV-3. Multiplicative partition of species and generic diversity among aquatic habitats in sixteen national parks, based on resampling (n=100) of presence-absence matrix. Standard errors given in parentheses.

Presence-Absence Matrix (q=0)

species	α	β	γ	genera	α	β	γ
total	14.25 (0.07)	20.78 (0.26)	296(2.53)	total	9.82 (0.05)	6.42 (0.11)	63 (0.93)
stream	14.69 (0.09)	16.27 (0.22)	239 (2.8)	stream	10.13 (0.07)	5.82 (0.12)	59 (0.99)
bog	17.53 (0.35)	7.64 (0.2)	134 (3.2)	bog	11.88 (0.24)	3.62 (0.12)	43 (1.28)
river	18.84 (0.24)	6.95 (0.13)	131 (2.99)	river	11.19 (0.16)	3.75 (0.12)	42 (1.42)
seep	10.61 (0.16)	13.84 (0.4)	147 (3.04)	seep	8.48 (0.12)	5.9 (0.18)	50 (1.11)
pond	12.29 (0.18)	11.8 (0.27)	145 (2.48)	pond	8.2 (0.13)	5.61 (0.19)	46 (1.33)

Table IV-4. Partitioning of alpha (α), beta (β) and gamma (γ) diversity among parks for species and genus abundances. Standard error of estimate is given in parentheses.

Abundance (q=1) species	α	β	γ
total	6.13 (0.05)	14.83 (0.2)	90.92(1.20)
abli	5.33 (0.41)	1.65 (0.09)	8.79 (0.6)
biso	6.37 (0.14)	4.7 (0.09)	29.9 (0.79)
blri	7.31 (0.11)	8.31 (0.21)	60.75 (1.37)
chch	6.97 (0.25)	3.9 (0.15)	27.21 (1.07)
cowp	5.13 (0.19)	3.25 (0.16)	16.69 (0.99)
cuga	6.54 (0.21)	4.9 (0.17)	32.08 (0.82)
fodo	5.58 (0.27)	1.79 (0.11)	9.96 (0.79)
grsm	4.47 (0.07)	5.58 (0.12)	24.93 (0.53)
guco	2.91 (0.14)	1.69 (0.07)	4.9 (0.33)
kimo	14.55 (0.34)	3.2 (0.35)	46.58 (2.27)
liri	5.58 (0.21)	4.52 (0.2)	25.21 (1.15)
maca	4.81 (0.17)	6.56 (0.26)	31.56 (1.13)
nisi	6.05 (0.17)	3.75 (0.12)	22.66 (0.81)
obri	8.99 (0.27)	3.6 (0.09)	32.34 (1.19)
shil	4.7 (0.12)	3.99 (0.13)	18.73 (0.79)
stri	7.96 (0.29)	1.6 (0.05)	12.76 (0.54)

Abundance (q=1) genus	α	β	γ
total	4.63 (0.03)	5.04 (0.05)	23.38 (0.23)
abli	3.92 (0.32)	1.57 (0.1)	6.16 (0.4)
biso	4.22 (0.06)	3.15 (0.06)	13.29 (0.28)
blri	5.45 (0.07)	4.1 (0.08)	22.28 (0.34)
chch	4.3 (0.15)	2.48 (0.1)	10.67 (0.44)
cowp	4.38 (0.16)	2.28 (0.11)	9.97 (0.46)
cuga	4.87 (0.14)	2.4 (0.06)	11.69 (0.35)
fodo	4.23 (0.19)	1.45 (0.1)	6.13 (0.46)
grsm	3.55 (0.07)	4.02 (0.07)	14.28 (0.24)
guco	2.76 (0.12)	1.58 (0.07)	4.37 (0.23)
kimo	10.15 (0.29)	1.85 (0.13)	18.73 (0.87)
liri	4.16 (0.16)	2.79 (0.16)	11.6 (0.61)
maca	4.07 (0.14)	3.67 (0.18)	14.96 (0.54)
nisi	3.66 (0.1)	2.06 (0.06)	7.55 (0.23)
obri	6.13 (0.2)	2.25 (0.07)	13.75 (0.54)
shil	4.05 (0.14)	2.77 (0.1)	11.24 (0.44)
stri	5.64 (0.18)	1.31 (0.04)	7.38 (0.29)

Table IV-5. Partitioning of alpha (α), beta (β) and gamma (γ) diversity among parks for species and genus presence-absence data. Standard error of estimate is given in parentheses.

Presence-Absence (q=0)				Presence-Absence (q=0)			
species	α	β	γ	genus	α	β	γ
total	14.25 (0.07)	20.78 (0.26)	296(2.53)	total	9.82 (0.05)	6.42 (0.11)	63 (0.93)
abli	10 (0.65)	1.8 (0.05)	18 (1.33)	abli	6.5 (0.5)	1.54 (0.1)	10 (0.79)
biso	18.36 (0.26)	5.77 (0.12)	106 (2.29)	biso	11.22 (0.17)	3.47 (0.11)	39 (1.18)
blri	15.67 (0.16)	12.07 (0.24)	189 (3.07)	blri	11.07 (0.11)	4.88 (0.11)	54 (0.88)
chch	18.22 (0.38)	4.07 (0.11)	74 (2.12)	chch	10.89 (0.31)	2.76 (0.11)	30 (1.04)
cowp	9.07 (0.25)	5.18 (0.23)	47 (2.07)	cowp	7.86 (0.24)	3.82 (0.25)	30 (1.48)
cuga	14.27 (0.33)	5.47 (0.16)	78 (2.48)	cuga	9.87 (0.22)	3.04 (0.14)	30 (1.21)
fodo	10.43 (0.31)	3.26 (0.12)	34 (1.41)	fodo	8.14 (0.27)	1.96 (0.1)	16 (0.91)
grsm	13.74 (0.18)	6.62 (0.19)	91 (2.06)	grsm	9.43 (0.14)	4.15 (0.13)	39 (0.87)
guco	6.67 (0.28)	2.7 (0.15)	18 (1.1)	guco	5.5 (0.24)	2 (0.14)	11 (0.75)
kimo	15.57 (0.37)	4.43 (0.29)	69 (2.67)	kimo	11.64 (0.29)	2.32 (0.15)	27 (1.01)
liri	13.14 (0.35)	5.86 (0.2)	77 (2.84)	liri	8.79 (0.26)	3.41 (0.18)	30 (1.47)
maca	10.75 (0.24)	8 (0.22)	86 (2.94)	maca	8.25 (0.19)	4.36 (0.19)	36 (1.34)
nisi	13.42 (0.25)	5.29 (0.16)	71 (2.06)	nisi	8.95 (0.19)	3.13 (0.18)	28 (1.27)
obri	22.56 (0.49)	4.17 (0.1)	94 (2.24)	obri	13.44 (0.34)	2.31 (0.08)	31 (0.8)
shil	9.53 (0.27)	5.14 (0.21)	49 (1.78)	shil	7.87 (0.21)	3.05 (0.17)	24 (1.07)
stri	21.75 (0.58)	1.93 (0.07)	42 (1.54)	stri	15 (0.53)	1.27 (0.06)	19 (0.78)

Table IV-6. Summary statistics for t-test on hypothesis on two measures of community dissimilarity in headwater and mid-order streams in Great Smoky Mountains and Blue Ridge Parkway.

Similarity measure		**Sorensen**		**Jaccard**	
Park	**Taxa**	**t (df)**	***p***	**t (df)**	***p***
GRSM	Species	10.08 (383.2)	<0.0001	9.82 (334.9)	<0.0001
	Genera	12.25 (415.1)	<0.0001	11.94 (377.2)	<0.0001
BLRI	Species	-0.41 (9.12)	0.69	-0.36 (9.13)	0.73
	Genera	-0.73 (9.09)	0.482	-0.6 (9.1)	0.56

GENERAL CONCLUSIONS

CHAPTER II: A METHOD FOR PREDICTING *IN SITU* CLIMATE REFUGIA AND FUTURE CONNECTIVITY IN PROTECTED AREA NETWORKS

- The objective of this chapter was to outline how techniques adapted from species distribution modeling can be used to assess the ecological performance of protected areas, independent of the species occurring in these protected areas.

- I used MaxEnt, a program developed for species distribution and ecological niche modeling, to build models that predict the geographic distribution of the climates occurring within protected areas. Projecting these models into future conditions estimates the potential geographic location of *in situ* climate refugia, or where climates currently occurring in protected areas persist into future conditions.

- The "climate footprint" is the geographic extent of the climate occurring in a protected area, and provides a spatial context for analyzing the climatic performance of protected areas. Change in the area or extent of the climate footprint of a protected area might have certain implications for management options, or more generally may predict areas where species interactions or distributions may shift more rapidly or unpredictably.

- Common climate-envelope based predictions of the future distributions of species are predicated upon assumptions which may not be strongly supported by empirical

evidence (e.g., that climatic features are strong determinants of the distribution of species). Analyses of the climate footprint of protected areas may avoid these assumptions and provide an objective evaluation of the domain of climatic changes likely to be experienced in protected areas under future climate scenarios.

- Models predict that, for many national parks in the conterminous 48 United States, current climate configurations will be replaced by non-analog climates by 2050. Ecological responses to these shifts are likely to involve changes in the direction and magnitude of species interactions.

CHAPTER III: PREVALENCE OF IMPERILED AQUATIC INSECT SPECIES IN A HIGH QUALITY PROTECTED AREA NETWORK

- Protected area networks vary in the amount of protection afforded to plants, animals or landscapes. National parks, which prohibit many land uses permitted in other protected areas, might be expected to provide enhanced levels of protection to species occurring on these lands.
- Many aquatic insect species are considered rare over parts or all of their geographic range. States vary in species richness of aquatic insect species, and turnover among states is defined along a gradient of geographic distance.
- National parks in the southeastern highlands are habitat for many aquatic insect species of varying rankings of perceived threat or imperilment. Large parks have

more species, and a strong temperature and precipitation gradient across parks is correlated with turnover of species along the spatial gradient.

- Rare species of aquatic insects are less prevalent in national parks than would be expected from a random draw from the regional source pool, as defined by published or compiled state lists of aquatic insect species.
- Description of aquatic insect species geographic ranges, based on species occurrences, will be critical to further refinements of regional source pools and macroecological investigations of aquatic insect species diversity.

CHAPTER IV: CADDISFLY SPECIES TURNOVER ALONG HYDROLOGICAL GRADIENTS AND VARYING SOURCE POOLS

- An understanding of species richness or diversity among sites or along gradients is a fundamental goal of ecology. Data on the distribution and abundance of aquatic insects is used to assess the quality of streams, rivers and lakes across the world.
- Although many studies cite the River Continuum Concept (RCC) as an example of a theoretical prediction of species richness or diversity of stream organisms, the RCC makes no such predictions. However, the RCC is a validated model of the structure of gradients of resource availability and biotic and abiotic parameters, some of which certainly constrain species richness and diversity at sites.
- Studies purporting to measure the turnover of species among sites, or along spatial/environmental gradients, have not actually measured the turnover of

species. Instead, these studies have analyzed turnover of operational taxonomic units (some of which might be species, others are genera or families of insects).

- The taxonomic imprecision inherent in data obtained from immature or larval specimens not only underestimates species richness and diversity but also has the potential to confound potential sources of turnover along these gradients, or to compare patterns of richness and diversity among streams at different positions along the longitudinal continuum.
- I sampled aquatic habitats in 15 national parks using blacklight traps during summer flight periods of adult caddisflies.
- Parks vary in the distribution of available habitat types, necessarily constraining patterns of species richness and turnover among sites. Stream habitats are the most diverse, in terms of total species richness, turnover among sites and the per-capita rate of species accumulation as a function of sampling additional sites.
- Using data on caddisfly genera obscures some patterns of species turnover among sites. However, turnover among caddisfly genera remains strongly significant along the hydrological gradient of headwaters to larger streams within a single watershed. Since caddisfly genera are generally ecologically distinct, this is consistent with RCC theory which predicts functional responses of ecological trait syndromes to resource gradients.
- Species turnover along hydrological gradients is a process distinct from turnover associated with changes in source pools. Comparisons of sites along a transect

(across multiple source pools) does not show a significant difference in the amount of species turnover between headwater streams and mid-order streams.

- Species richness, within a single watershed in the Great Smoky Mountains National Park (presumably sharing the same source pool), is lower in headwater streams than larger streams. At sites along a latitudinal transect traversing multiple source pools (the Blue Ridge Parkway in North Carolina and Virginia), species richness is not different among headwaters and mid-order streams.
- Dispersal of aquatic insects remains a poorly understood phenomenon, but coordinated sampling of adult and larval aquatic insect assemblages may elucidate community assembly patterns that are currently beyond the scope of benthic investigations.

VITA

Jason Lesley Robinson was born in Buncombe County, North Carolina in 1977. Even from an early age, he had an intense fascination with streams and aquatic organisms, likely stemming from early exposure to the capture of large *Esox masquinongy* with his father and uncle Clyde. He attended A.C. Reynolds High School and fished nearly every trout stream in the upper French Broad watershed by his graduation in 1994. Jason then enrolled in the Fisheries and Wildlife Science program at N.C. State University in Raleigh, NC, where he became interested in the ecology of fishes, graduating in 1999. During that time, he spent several summers gaining research experience by working on fisheries projects with graduate students in coastal and mountain systems. He took several field courses at Highlands Biological Station that cemented his research interests in stream ecology and then enrolled in the Graduate Program in Zoology at N.C. State to work with Dr. Peter Rand. His M.S. topic was on the distribution of rare fishes in streams along the Blue Ridge Escarpment in the upper Savannah River basin in western NC, lands where he had hunted and fished as a teenager but was now transferred to the state of NC as the new Jocassee Gorges State Park. During this time Jason began thinking about historical biogeography and how landscape patterns have constrained the possible configurations of aquatic communities in the Appalachians, topics he would continue to consider until his doctoral research years later. In the meantime, he gained valuable experience in the taxonomy of benthic macroinvertebrates and local contacts. Upon his graduation from NCSU in 2002 he spent several years working as a consultant in various capacities across western NC, flyfishing Davidson and Oconaluftee Rivers at

will, playing basketball, sleeping outside and hanging out with talented musicians as much as possible. During this time, he witnessed the last show played by Jimmy Martin. In 2005, he and friends put on Squirrelfest, a music festival that will likely never be equaled. At this point, Jason took a research position at the University of Tennessee in the lab of Nate Sanders, working on a project that would eventually become his dissertation research. Here his dalliance with aquatic insects became a full-blown obsession; thanks to the tutelage of Chuck Parker and David Etnier he was fortunate enough to gain expert experience in the systematics of Trichoptera and broader familiarity with many other orders of insects. He entered the Ph.D. program in Ecology and Evolutionary Biology at the University of Tennessee in fall 2007, where he gained skills in species distribution modeling, honed his teaching skills and played bluegrass music with his band Catfish Mercury Load. After completing his dissertation, Jason took a postdoctoral position at the Illinois Natural History Survey at the University of Illinois at Urbana-Champaign. In his spare time, Jason loves to hunt, fish and harvest edible mushrooms and plants with his wife Jill, son Fox and daughter Rainer. Whenever possible, he plays old time and bluegrass music, contemplates questions too large to answer and work as an advocate for science, scientific education and biodiversity. In rare moments of quiet solitude, he sits silently and watches spiders build webs or listens to worms crawl in the leaf litter and thinks about how he is so lucky.